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THE SYSTEMATICS OF FOSSIL AND RECENT SALAMANDERS (AMPHIBIA: CAUDATA), WITH SPECIAL REFERENCE TO THE VERTEBRAL COLUMN AND TRUNK MUSCULATURE

by

© BRUCE G. NAYLOR

A THESIS

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IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE
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EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "THE SYSTEMATICS OF FOSSIL AND RECENT SALAMANDERS (AMPHIBIA: CAUDATA), WITH SPECIAL REFERENCE TO THE VERTEBRAL COLUMN AND TRUNK MUSCULATURE" submitted by Bruce G. Naylor in partial fulfilment of the requirements for the degree of Doctor of Philosophy in Vertebrate Paleontology.

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ABSTRACT

New information allowing for better understanding of fossil material and phylogenetic relationships of the order Caudata was obtained by comparative anatomical studies, primarily of the vertebral column and trunk musculature. Characters for phylogenetic investigation are suggested to be part of an adapted functional complex, to be present in higher and lower taxa (for ex-group and in-group comparisons), and to be preservable in fossil specimens. The evolutionary approach is used as the most reasonable basis for biological classification, cladistics and phenetics being rejected as philosophies for this study.

Functional inferences from the new data concern the development of opisthocoely and the presence of elongate rib-bearers in the axial myosepta. Intra- and interfamilial relationships are analyzed and phylogenetic hypotheses proposed. Two suborders are named and defined: the primitive Archaeocaudata, including the Cryptobranchoidea (Hynobiidae and Ambystomatidae), and the Prosirenidae as Archaeocaudata *incertae sedis*; and the more derived Neocaudata, including the Proteoidea (Batrachosauroididae and Proteidae), Plethodontoidea (Plethodontidae), and Salamandroidea (Sirenidae and Salamandridae).

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INTRODUCTION

Owing to paucity of the fossil record and the extensive occurrence of neoteny and structural simplification, phylogenetic relationships of the families of salamanders have long been uncertain. Although Wake's (1966) classification of the Caudata has been generally accepted (but see Edwards 1976), certain areas of controversy remain. Furthermore, little new information has been forthcoming to either corroborate or controvert Wake's scheme. The major aim of this study is to provide new data bearing on the relationships of salamanders. As noted by Larsen (1963), uncertainty exists at both supra- and infrafamilial levels. My work is a continuation of the investigations of investigators such as Dunn (1926), Noble (1931), Herre (1935b), Tihen (1958), Estes (1965b), Wake (1966), Wake and Özeti (1969), and Edwards (1976), who have each studied the Caudata at various taxonomic levels.

Although paleontology necessarily remains the prime source of information for those working on phylogenetic relationships, salamanders present serious difficulties for a purely paleontological approach. The fossil record of these amphibians is sparse and demonstrably biased in favour of derived, neotenic lineages (see Estes 1965b). Although of major importance, the known fossils have little to say about the origins and relationships of the living families (perhaps excepting the Proteidae). Rather, they must be fitted into schemes based on the Recent taxa. Bizarre results obtain if the fossil taxa are interpreted as truly primitive (e.g., Vandel 1966).

Fitting the fossil taxa into the Recent framework has proven difficult for a number of reasons. With a few notable exceptions (e.g., *Hylaeobatrachus*, *Opisthotriton*, *Palaeoproteus*, and *Ramonellus*), fossils are represented by isolated skeletal elements, which must be properly interpreted and associated in order to gain an appreciation of the entire organism. A precise knowledge of the osteology of living species is, therefore, necessary. Type specimens tend almost invariably to be isolated vertebrae, with the other elements being referred with greater or lesser certainty. Problems have arisen owing to lack of detailed osteological and myological knowledge of the trunk region of living salamanders. This has necessitated a basically empirical approach to usage of vertebrae in the study and classification of fossil taxa.

To satisfy the goals of the present study it was first necessary to survey the topographic features of the vertebrae throughout the order. However, after this was done, it became evident that a strictly osteological approach was not sufficient. Vertebrae owe their various shapes and accessory processes to the ways in which they function in locomotion. This being so, detailed dissection and description of the trunk musculature were necessary. Owing to a considerable amount of (unforeseen) diversity within certain families (notably the Plethodontidae and Salamandridae), as many genera were studied as possible. The results reported below document a tremendous wealth of inter- and intrafamilial variation and a large amount of phylogenetically and functionally significant data present in the trunk region. This information is presented in the form of anatomical descriptions of the vertebral column and trunk musculature, and in drawings. The approaches, techniques used, and specimens studied are discussed at the beginnings of the osteological and myological sections below.

Data gained from this study were then available for application to functional, phylogenetic, and paleontological problems. It proved possible to produce more concrete theories as to the origin of opisthocoely in salamanders and the relationships of certain families (notably amphiumids, proteids, batrachosauroidids, plethodontids, salamandrids, and sirenids). In light of the new information, previously studied characters and character complexes came to be more readily (and, hopefully, more realistically) interpretable, especially with respect to the fossil record.

A brief note on the terms paedomorphosis, paedogenesis (= progenesis of Gould 1977), and neoteny is necessary, as they are of major relevance to salamanders. These terms have been a source of some confusion and are often used interchangeably. Paedomorphosis is an evolutionary phenomenon, resulting from the retention of larval (or juvenile) traits of an ancestor in the adult of a descendant (see de Beer 1958). Paedogenesis and neoteny have been utilized in quite different senses by various authors. I use these terms as follows (see Wilbur and Collins 1973):

1. Paedogenesis: obligatory partial or total retention of larval features, such as in *Necturus* or *Siren*. The larval traits are, therefore, genetically fixed and the sexually mature animal cannot metamorphose from the larval state.

2. Neoteny: the facultative maintenance of the larval state in sexually mature animals, such as in *Ambystoma* and *Notophthalmus*.

In this situation, reproduction in the larval state is simply an alternative adaptive strategy.

These usages depart from those of de Beer (1958), who defined paedogenesis as the acceleration of the sexual organs with respect to the somatic tissues, whereas neoteny was the retention of larval structures and form (hence retardation of the somatic tissues). Gould (1977) has unnecessarily substituted the term progenesis for paedomorphosis, but otherwise retains de Beer's usages. In spite of Gould's attempted defence, the definitions of de Beer have little profound meaning or difference, and are operationally unworkable.

Abbreviations

Abbreviations of institutions are as follows:

AMNH - American Museum of Natural History, New York.

SMNH - Saskatchewan Museum of Natural History, Regina.

UA - The University of Alberta, Edmonton (Vertebrate Paleontology Collections).

UA-MZ - The University of Alberta, Museum of Zoology, Edmonton.

UC-MVZ - University of California at Berkeley, Museum of Vertebrate Zoology.

UW-RCS - University of Washington, R.C. Snyder.

Abbreviations used in Figures are as follows:

1) Vertebral:
    1a - first alar process.
    2a - second alar process.
    3a - third alar process.

ab - anterior basapophysis.

acn - anterior condyle.

al - anterior lamella.

alp - aliform process.

hap - hypapophysis or subcentral keel.

hrp - hyperapophysis or neural spine.

izc - interzygapophyseal crest.

nc - neural crest (neural spine of authors).

ncn - neural canal.

pb - posterior basapophysis.

pct - posterior cotyle.

ptp - pterygapophysis.

pz - postzygapophysis.

prz - prezygapophysis.

sbf - subcentral foramen.

spc - spinal nerve canal.

T1 - first trunk vertebra or second cervical.

T2 - second trunk vertebra, etc.

tp - transverse process.

vc - vertebrarterial canal.

2) Anatomical:

a.f. - anterior flexure.

a.t. - adipose tissue.

b.m. - anterior basapophyseal muscle (Archaeocaudata).

'b.' m. - "basapophyseal" muscle (*Siren*).

'b.' s. - "basapophyseal" septum (*Siren*).

b.v. - blood vessel.

c.c. - centre of calcification.

c.t. - connective tissue.

d.p.f. - deep posterior flexure.

d.r.p. - deep part of the *rectus abdominus profundus*.

d.t. - *dorsalis trunci*.

E. - epaxial musculature.

fa. - fascia.

g. - mid-dorsal gland (*Rhyacotriton*).

H. - hypaxial musculature.

h.m. - hyperapophyseal muscle.

ic. - intercostal musculature.

i.s. - internal septum.

it. - *intertransversus*.

iv-1, iv-2, iv-3 - intervertebral muscle blocks (*Amphiuma*).

iv-5 - intervertebral muscle block (*Siren*).

m.b.m. - main body of myomere.

o.e. - *obliquus externus*.

o.e.p. - *obliquus externus profundus*.

o.e.s. - *obliquus externus superficialis*.

o.i. - *obliquus internus*.

p.a.f. - primary anterior flexure (*Amphiuma*).

p.b.m. - posterior basapophyseal muscle (Neocaudata).

p.f. - posterior flexure.

p.m. - pterygapophyseal muscle (*Desmognathus*).

p.s.m. - posterior septum of expaxial myomere.

ra. - *rectus abdominus*.

'r.' - area of *rectus abdominus* (*Siren*).

r.l. - *rectus lateralis*.

r.p. - *rectus abdominus profundus*.

r.s. - *rectus abdominus superficialis*.

s. - skin.

s.a.f. - i) septum of anterior flexure.
ii) secondary anterior flexure (*Amphiuma*).

s.m. - scapular musculature.

s.p.f. - septum of posterior flexure (Neocaudata).

sp.n. - spinal nerve.

s.r.p. - superficial part of *rectus abdominus profundus*.

s.v. - *subvertebralis*.

sv - septal-vertebral muscle block (*Amphiuma*).

t.p.f. - transverse process flexure (Archaeocaudata).

t.p.m. - transverse process muscle.

tr. - *transversus*.

v.sv. - ventral layer of *subvertebralis*.

z.s. - zygapophyseal septum (*Necturus*).

Chapter I

DESCRIPTIONS OF THE VERTEBRAL COLUMN

A. Introduction

This section comprises descriptions of the vertebral columns of representative species of each family of living salamanders. Details of the structure and variation of the vertebral column have not been studied to the same extent as have other parts of the skeleton. Wiedersheim (1875) described and figured the vertebral columns of *Salamandrina* and *Hydromantes*, while Riese (1891) provided descriptions of the column of *Tylototriton*. Ontogenetic development has been treated by Mauger (1962, *Pleurodeles waltli*), Worthington (1971, *Ambystoma opacum*), and Wake and Lawson (1973, *Eurycea bislineata*). Estes (1964, 1969a,b,c) provides extensive descriptions of the vertebrae of fossil taxa. . Wake (1970) briefly considered salamanders in his general review of vertebral evolution within the Amphibia. Worthington and Wake (1972) quantified variation along the column in species of *Ambystoma*, *Taricha*, *Notophthalmus*, *Chiropterotriton*, *Desmognathus*, *Eurycea*, and *Plethodon*. Although this latter study, if expanded, is potentially of interest to investigators of locomotion, it has little direct applicability to phylogenetic reconstruction and paleontological study.

Owing to the widespread occurrence of paedomorphosis (evolution by means of foetalization) within the Caudata, studies of the sort carried out by Worthington (1971) on *Ambystoma* and by Wake and Lawson (1973) on

Eurycea are of major interest and informational content with respect to phylogenetic analysis. Most recently, Edwards (1976) has documented the patterns of the spinal nerve exits throughout the Caudata. This study is important in that it deals with a feature readily observable in both fossil and Recent material. Further, for whatever reason, these patterns correlate well with other anatomical data, allowing them to have major input into classification and phylogenetic analysis. In spite of these efforts, work on the structure of Recent salamanders is still necessary. I suggest that this must be of the "classical" sort of comparative description (see Zangerl 1948), which provides the data necessary to phylogenetic study.

Paleontological studies of salamanders are, by the nature of the fossil record, heavily dependent on vertebrae and the majority of fossil taxa are based on trunk vertebrae. Owing to the spotty nature of the fossil record of the Caudata, the living species must be studied in order to understand the fossil. There is a great deal of vertebral diversity within and between the families of living salamanders. The variation between taxa is often directly related to the structure of the associated trunk musculature (see the following descriptions), although correlations are sometimes not obvious. Given the diversity, work on fossil material can only proceed from a clear understanding of the Recent. Otherwise, of necessity, paleontological systematics is typological and empirical, with "diagnostic" characters chosen on the basis of intuition and comparison of the, usually isolated, fossil material.

For each species a complete description of the atlas, second cervical (the first trunk vertebra, T1), a mid-trunk vertebra, the sacrum (when present), and a haemal vertebra (generally the third one of those having a complete haemal arch) is provided. For these vertebrae, the following parts were considered and described in each species, where applicable:

1. Centrum: anterior cotyle or condyle
   posterior cotyle
   subcentral foramina
   hypapophysis (= subcentral keel)
   basapophyses
2. Neural arch: neural canal
   roof of the neural arch
   neural crest
   hyperapophysis (= neural spine)
   spinal nerve foramina
   zygapophyses
3. Haemal arch.
4. Transverse processes (= rib-bearers).

Additionally, variation along the entire column for the following parts is described: cotyle and condyle, hypapophyseal structures, neural arch (rarely used), neural crest and hyperapophysis, zygapophyses, and transverse processes.

The terms used in this section are provided in Figure 1 (see also Abbreviations), and generally are those currently accepted. The neural crest has been called the neural spine by other authors. However, the latter term is potentially or actually confused with the posterior portion of the neural arch, which is here termed the hyperapophysis.

The term transverse process (or, if applicable, rib-bearer) is utilized owing to its use in the literature. The two processes of each rib-bearer are simply called the dorsal (diapophysis of authors) and ventral (parapophysis of authors) arms because of uncertainty as to their true homologies (see also Gamble 1922). Wake's (1966) designation for the process on the dorsal surface of each postzygapophysis in desmognathines, the pterygapophysis, is used. The designation aliform process is used in the sense of Auffenberg (1959), but with extension to the salamandrid newts as well as sirenids (see also Estes 1964, 1965b). Finally, I term the accessory flanges from the transverse processes of *Siren* the first, second, and third alar processes (see Fig. 1). The third alar process is unique to sirenids, but the first and second alar processes sometimes form the ventral lamellae in other salamanders.

B. Descriptions

i) Family Hynobiidae Cope 1859

Pachypalaminus boulengeri Thompson 1912

Specimens.- One dry skeleton (UA 14322) and one cleared and stained specimen (UA 14412).

ATLAS. The anterior cotyles are medium-sized, irregular ovals extending laterally on either side of the odontoid process. They are situated largely below the neural canal and their dorsal edges are tilted posteriorly. Articular facets are very gently concave. The odontoid process is short and thin, but wide and with the dorsal surface concave for passage of the nerve cord. There is a ventral articular facet on the odontoid and the process is located centrally with respect to the height of the anterior cotyles. The posterior cotyle is deeply concave with a large, centrally located, notochordal pit. The cotyle is teardrop-shaped with a flattened ventral border, which is produced somewhat posteriorly. A pair of small posterior basapophyses is present.

The neural canal is small and triangular in anterior view. The neural arch is robust, with a steeply sloping roof, and pierced by a foramen behind each anterior cotyle. Excepting a thin anterior connection in the larger specimen, the roof of the neural arch is not ossified, being finished in cartilage even in relatively large adults. There is no ossified hyperapophysis.

A low ridge extends from each anterior cotyle, posteromedially along the base of the centrum. The posterior zygapophyseal facets are large, long teardrops extending posteriorly and slightly laterally. The lateral edges are raised dorsally to a small degree. Transverse processes are absent.

SECOND CERVICAL (T1). The anterior cotyle is medium-sized, circular in end view, and coated with a small amount of uniform infilling of calcified tissue. The dorsal and ventral rims project somewhat anteriorly. The central notochordal pit is wide and deep. The posterior cotyle is large and subcircular in end view, its ventral border extending posteroventrally. There is a small amount of uniform infilling, and the notochordal pit is large and centrally located.

There is a slight trace of a subcentral keel, and subcentral foramina are variably developed. Basapophyses are not evident.

In anterior view the neural canal is small and has the appearance of an almost perfect upside-down heart shape. The roof is in the form of an inverted V. Foramina for the exit of spinal nerves are lacking. A robust, low crest extends the length of the roof. The neural arch ends posteriorly in a low, broad boss, which is little raised above the posterior zygapophyses and ends between them. There are no facets for the insertion of hyperapophyseal muscles.

The articular facets of the prezygapophyses are large, elongate ovals extended anterolaterally. The lateral borders are raised dorsally and the facets originate below the top of the neural arch. The posterior zygapophyseal facets are large and oyster-shaped. They extend anteroposteriorly and the lateral borders are deflected dorsally.

Transverse processes are relatively short, but robust. They are distinctly bicipital, but confluent. The processes originate midcentrally and are angled gently posterolaterally with the larger, dorsal arms being posterior to the ventral. Alar processes are absent, but there are small, thin anterior and posterior webs of bone buttressing the ventral arms to the centrum.

The second cervical is a robust, short, high vertebra.

TRUNK VERTEBRA (T7, see Fig. 2). The seventh trunk vertebra is well-ossified, but long, low, and slender. The subcircular anterior cotyle is medium-sized, with a small amount of uniform infilling. The ventral rim is thickened in the basapophyseal area. A deep and wide notochordal pit is located centrally. The posterior cotyle has the form of a broad teardrop with its ventral rim extending posteroventrally and the dorsal rim flattened. The notochordal pit is large. A faint ridge on the posterior one third of the centrum represents the hypapophysis. Subcentral foramina are lacking and there is a pair of small anterior basapophyses.

The neural canal is small, and low and wide. The roof is arched and foramina for spinal nerves are absent. The neural crest is represented by a faint ridge occupying the central half of the roof of the neural arch. The hyperapophysis is a low, broad boss only slightly raised above the posterior zygapophyses and not projecting backwards. The facets of the anterior zygapophyses are large, irregular ovals, aligned anterolaterally with their lateral edges upswept. The posterior zygapophyses are in the form of broad teardrops, aligned anteroposteriorly with a slight posterolateral component. The facets are inclined dorsolaterally, and are concave dorsally.

The transverse processes are thin, short, and slightly swept posteriorly. The arms are close together but diverge slightly so as to separate distally. The transverse processes originate midcentrally, with the dorsal arms somewhat posterior of the ventral, such that the whole transverse process is tilted from the vertical. Alar processes are absent. A small, well-developed vertebrarterial foramen pierces the ventral arm of each transverse process.

SACRUM (T19). The sacrum continues the trend for decrease in vertebral size along the posterior portion of the trunk and into the tail. Its sole distinguishing feature is the disproportionate size of the transverse processes.

The anterior cotyle is medium-sized, appearing as a laterally elongate oval in anterior view. A small amount of calcified tissue uniformly coats the cotyle internally. There is a large, centrally located, notochordal pit. The posterior cotyle is slightly oval in the horizontal plane, with the ventral rim produced posteroventrally. There is a large central notochordal pit. Basapophyses, hypapophysis, and subcentral foramina are absent.

The neural canal is larger than in the central trunk vertebrae, and appears low and wide in anterior view. The roof of the neural arch is flat and spinal nerve foramina are absent. A neural crest is absent. The neural process (hyperapophysis) is low and wide, as in the trunk vertebrae, but projects slightly more posterodorsally, showing the beginnings of the trend culminating in the long neural process of the caudal series. The prezygapophyseal facets are large, irregular circles with the lateral edges slightly upturned. The facets of the postzygapophyses are irregular ovals, aligned posterolaterally with the lateral and medial edges slightly tipped ventrally.

Transverse processes are short, but robust and very wide distally. The arms are confluent, but bicipital, with the dorsal smaller than the ventral. Transverse processes originate midcentrally and extend posterolaterally in the vertical plane. Small anterior alar processes are present and a small vertebrarterial canal pierces each transverse process next to the centrum.

HAEMAL VERTEBRA (H3). The anterior cotyle is large and oval in the horizontal plane. There is a small amount of uniform infilling and a large notochordal pit. The posterior cotyle differs from the anterior in being subcircular with the ventral rim extended somewhat posteriorly. The haemal arch is well-developed, arising along the central two thirds of the centrum. There is a large circular haemal canal and each lateral wall is pierced by one or two small foramina. A haemal crest is absent. The haemal process extends posteroventrally, is long, and ends bluntly.

There is a small, low, and wide neural canal with a domed roof. A neural crest is not present. The hyperapophysis is short, not quite projecting to the ends of the posterior zygapophyses. It is wide and robust, lacking facets for muscle attachment. Spinal nerve foramina are absent. Prezygapophyseal facets are large, irregular ovals disposed anterolaterally with the lateral edges inclined dorsally. Postzygapophyseal facets are broad teardrops of irregular outline. They extend anteroposteriorly and the medial and lateral edges are slightly inclined downwards.

Well-developed transverse processes are present. They are long, unicipital rods originating from the wall of the neural arch just above the midpoint of the centrum. They are directed gently posteriorly and ventrally. Alar processes and vertebrarterial canals are lacking.

VARIATION ALONG THE COLUMN. *1. Cotyles.*- The centra are deeply amphicoelous throughout the column, with a thin layer of granular calcified tissue internally. There is a small mid-central plug dividing the cotyles in larger individuals. The chordal foramen is often slightly dorsal of the centre, although located centrally in those centra that are most dorsoventrally compressed. In the pectoral region (T1-T3), the anterior cotyle is subcircular. Posterior to these, the cotyle is a laterally elongate oval, especially in the posterior half of the trunk. The sacrum and caudosacrals retain this dorsoventral compression of the anterior cotyle, whereas that of the haemal vertebrae, although still oval, tends to be subcircular. There is a tendency for the dorsal and ventral rims of the anterior cotyle to project forward, producing an excavation of the lateral rim. This is best developed in the first few haemal vertebrae.

The posterior cotyle to some extent mirrors the corresponding anterior cotyle. However, each has a distinct posteroventral extension of the ventral rim, which gives the tendency to a very broad teardrop shape in posterior view.

2. *Hypopophyseal structures*.- Excepting a faint subcentral ridge in the trunk region, a subcentral keel is lacking. The atlas has a pair of small posterior basapophyses, but such are lacking from T1 and T2. Posterior to this, anterior basapophyses appear. These are located ventrolaterally on the anterior cotyle, which often has the ventral rim somewhat thickened in the vertebrae immediately posterior to the pectoral girdle. Discrete anterior basapophyses are present throughout the trunk but are lacking from the sacrum and caudosacrals.

The third postsacral vertebra bears the first haemal arch, less perfectly formed than those further posterior, but with a well-developed haemal process extending posteroventrally. Behind this first haemal vertebra (H1), the haemal arch extends most of the length of the centrum. There are no crests or flanges developed, the arch being smooth. The haemal process is robust, extending posteroventrally to the same extent as the hyperapophysis of the same vertebra extends posterodorsally. The haemal canal is large and somewhat deeper than wide. The arch is variably pierced, usually only on one side, by a foramen for the exit of a blood vessel.

3. *Neural arch.*- The first four or five vertebrae including the atlas have a large neural canal, in the form of an inverted heart in anterior view. There is progressive decrease in the size of the canal moving from the atlas posteriorly. By T5 or T6 the canal is low and wide, presenting a kidney shape above the anterior cotyle. No marked increase in size is noticeable in the sacral region. The neural canal in the haemal series is similar in shape to that of the trunk, although, owing to a more flattened neural arch, the canal is roughly rectangular in anterior view.

In the trunk region, the roof of the neural arch is gently arched over the canal. The neural arch is a smoothly finished, robust structure, generally lacking auxiliary crests. Except in the atlas, foramina for spinal nerves are not present.

4. *Neural crest and hyperapophysis.*- T1 through T3 have a distinct, but low, neural crest anteriorly. Except for a faint ridge on the posterior part of the neural arch of the trunk vertebrae, a neural crest is not otherwise developed.

The hyperapophysis is of constant development in the trunk, sacral, and caudosacral vertebrae. It is low and broad, barely rising above the posterior zygapophyses. The hyperapophysis ends well before the hind edges of the posterior zygapophyses. It is in the form of a crescent, finished in calcified tissue, and lacking obvious crests for the insertion of hyperapophyseal septa and muscles. In the caudal vertebrae, the hyperapophysis is produced posterodorsally and shows a tendency to end bicipitally.

5. *Zygapophyses*.- The prezygapophyses are very large, extending anterolaterally out from the neural arch. The articular facets are somewhat elongate, irregularly shaped ovals. There is lateral uptilting, but this is nowhere markedly developed. The facets are almost horizontal in the sacral, postsacral, and caudal vertebrae. The prezygapophyses originate just slightly below the top of the roof of each neural arch.

The postzygapophyses are asymmetrically teardrop-shaped, extending posteriorly and slightly laterally. They are especially broad in the caudosacral and haemal regions. The facets are slightly upturned laterally, but also concave dorsally.

6. *Transverse processes*.- Transverse processes are distinctly bicipital, but not greatly divergent in the trunk region. Those in the area of the pectoral girdle (T1-T3) are robust and the dorsal and ventral rib-bearers are confluent distally. The transverse processes are here very powerful, and the dorsal rib-bearers are larger than the ventral. Posteriorly, the rib-bearers are separated distally and there is considerable variability in the relative sizes of the dorsal and ventral arms. The dorsal may be larger, the ventral may be larger, or they may be subequal. With the small sample at hand, there is no discernible pattern to this variation.

In the trunk region the transverse processes extend laterally and slightly posteriorly. The dorsal rib-bearers are set slightly behind the ventral. There is no development of accessory ridges and no trace of ventral lamellae associated with the rib-bearers. In the trunk region proper, the rib-bearers decrease in diameter, although not in length, posteriorly. Until the sacrum, they are separated distally, but there is little or no divergence of the rib-bearers. Although the trunk vertebrae have fully bicipital rib-bearers, those of the sacrum are almost completely confluent.

The transverse processes of the caudosacrals are elongate. Those of the first caudosacral are partially bicipital. Those posterior to this are unicipital, but still large, and extend laterally as far as those of the sacrum. The first three haemal vertebrae retain well-developed unicipital transverse processes, which decrease in size posteriorly. Over the next six or so haemals there is marked decrease in the size of the transverse processes, with respect to length and diameter. In this area, they are associated with the neural arch, whereas in the first few haemal and caudosacral vertebrae they originate from the lateral edge of the centrum. The following haemals lack transverse processes.

A small vertebrarterial canal pierces each transverse process through the ventral rib-bearer next to the centrum. These are largest in the first three trunk vertebrae.

Hynobius naevius (Temminck and Schlegel 1838)

Specimens.- One dry skeleton (UA 14321) and one cleared and stained specimen (UA 14411).

ATLAS. The anterior cotyles have large circular facets, which are vertical in lateral view. The cotyles are oriented such that their lateral edges are somewhat posterior to the medial edges. The articular surfaces are flat and situated ventral to the neural canal. The odontoid process is short, but broad and deeply concave dorsally for passage of the nerve cord. The process is situated midway down between the two cotyles. The posterior cotyle is small and subcircular, but the presence of a ventral thickening gives a superficial teardrop appearance. There is a small amount of uniform infilling and the notochordal area is deep and broad. A low, thin ridge extends from the posteromedial edge of each anterior cotyle to the terminus of the posterior cotyle. A pair of small, uniform subcentral foramina is present.

The neural canal is large and triangular in anterior view, with the anterior cotyles and odontoid process forming the base and the dorsomedially extending neural arch the sides. The neural arch is thin and pierced by a foramen posterior to each anterior cotyle. The roof extends into a low, broad neural crest, which runs the full length of the roof. A hyperapophysis is not developed, but a pair of low, small posteriorly facing facets occurs between the postzygapophyses. The postzygapophyseal facets are of medium size, in the shape of elongate teardrops extended anteroposteriorly, and with the lateral edges inclined dorsally.

Transverse processes are absent.

SECOND CERVICAL (T1). The anterior cotyle is medium-sized. Its dorsal surface is flattened, but it is otherwise subcircular in anterior view. The posterior cotyle is not large. In end view, it is a laterally elongate oval with the dorsal surface flatter than is the ventral. In both cotyles there is a small amount of uniform infilling. The notochordal pit is deep and wide in each, and the two cotyles are separated by a narrow plug of calcified tissue. The ventral edge of both cotyles is distinctly thickened and beneath the anterior cotyle is a small flange of bone. Hypapophyses and basapophyses are otherwise lacking and subcentral foramina are not developed.

The neural canal is expanded and wide, appearing rectangular in end view. The roof of the neural arch is wide and flat, and the walls lack foramina for spinal nerves. A distinct, low neural crest runs almost the total length of the neural arch. A neural process (hyperapophysis) is lacking, but a pair of large, posteriorly facing facets are found at the posterior terminus of the roof of the neural arch, above and between the posterior zygapophyses. The anterior zygapophyseal facets are small, irregular ovals extending anterolaterally, with the lateral edges slightly raised. The posterior zygapophyses are small, irregular ovals, disposed anteroposteriorly with the articular surfaces concave upwards.

The transverse processes are long and robust. The rib-bearers are bicipital with the two arms confluent along the entire length. The arms originate midcentrally and extend posterolaterally. The dorsal arms are deeper than the ventral and the transverse processes are wide distally. Small buttressing alar processes join the ventral arms to the centrum. Small, well-developed vertebrarterial canals are present.

TRUNK VERTEBRA (T7, see Fig. 3). The anterior and posterior cotyles are medium-sized relative to the size of the vertebra. The anterior cotyle is circular, but with a flattened dorsal rim. The posterior is subcircular, with the ventral rim projecting slightly posteroventrally.

Both cotyles have thickened ventral rims, a small amount of uniform infilling, and deep, large notochordal pits. More posterior trunk vertebrae have a chordal canal piercing the centrum. Subcentral foramina and basapophyses are lacking. There is a faint, low hypapophyseal ridge extending under the middle one half of the centrum.

The neural canal is large and hemispherical in anterior view. The roof is gently swollen and the arch lacks foramina for the exit of spinal nerves. There is a low, but distinct, neural crest extending posteriorly to the start of the hyperapophyseal area. A neural process is absent, the posterior part of the neural arch being thickened and dorsally flattened, with low, elongate facets facing posteriorly. Prezygapophyseal facets are oval teardrops, with an anterolateral placement and the lateral borders inclined dorsally. The posterior zygapophyses have smaller teardrop-shaped facets, which are disposed anteroposteriorly and with the articular surfaces concave upwards.

Transverse processes are thin and relatively short, being bicipital and slightly divergent. They originate midcentrally, high on the vertebra and extend posterolaterally. The smaller dorsal arms are slightly posterior to the ventral. Alar processes are absent and the vertebrarterial canals are extremely small.

SACRUM. There is some variability in the position of the sacrum, it being either the eighteenth or nineteenth trunk vertebra. The sacrum is small and, excepting the enlarged transverse processes, unmodified.

The anterior cotyle is medium-sized and in the form of a dorsoventrally flattened oval. The posterior cotyle is a broad teardrop with the ventral edge produced slightly posteriorly. There is a thin uniform layer of calcified tissue inside each cotyle. The notochord is only slightly constricted, but blocked off midcentrally by a small calcified plug. Subcentral foramina, basopophyses, and hypapophysis are absent.

The neural canal is low and wide, the roof above being wide and very gently arched. Foramina for spinal nerves are absent. The neural crest is represented by a faint ridge on the central half of the roof of the neural arch. The hyperapophysis is short and low, ending in a pair of small projections that do not extend beyond the posterior zygapophyses. Prezygapophyseal facets are relatively small teardrops. They extend anterolaterally and have the lateral edges upturned. The postzygapophyseal facets are oriented posterolaterally, in the form of irregular teardrops or ovals. The lateral borders are tilted dorsally.

Transverse processes are robust, originating just posterior of the middle part of the centrum and swept gently posterolaterally. They are unicipital and the distal ends are greatly expanded, especially dorsoventrally. Alar processes are lacking and a very small vertebrarterial canal pierces each transverse process next to the centrum.

HAEMAL VERTEBRA (H6). The haemals are thin, long vertebrae with few crests for the insertion of musculature. The anterior cotyle is large and dorsoventrally compressed. The posterior cotyle is subcircular, but with the dorsal rim flattened and the ventral rim projecting slightly posteriorly. In both, there is a small amount of calcified infilling, the notochord is little constricted, and the latter is divided by a thin calcified plug. The haemal arch, when present and complete, is poorly developed and composed of very thin bone. It covers the central three quarters of the centrum. The haemal canal is small and circular in end view. Each wall is pierced by a single foramen. A haemal crest is not present and the haemal process is short and ends bicipitally.

The neural canal is small, with a width somewhat greater than the height. The roof of the arch is narrow and gently domed. Foramina for spinal nerves are lacking. The neural crest is a low irregular ridge. The hyperapophysis is short, robust, and bicipital, ending at a level more or less at the ends of the posterior zygapophyses. Prezygapophyseal facets are large, elongate teardrops. They have a slight anterolateral component to their extension and the articular surfaces are concave. The postzygapophyses have facets in the form of smallish, long teardrops. They are situated posterolaterally and the lateral edges are tipped slightly dorsally.

The transverse processes are small unicipital rods extending from the wall of the neural arch just above the midpoint of the centrum. They extend laterally and slightly posteriorly for a short distance. Alar processes and vertebrarterial canals are absent.

VARIATION ALONG THE COLUMN. 1. *Cotyles*.- The anterior cotyle of T1 is approximately teardrop-shaped. All subsequent vertebrae have the anterior cotyle wider than high, although there is notable variation in shape: some are almost subcircular, others have pronounced dorsoventral flattening. The posterior cotyle exhibits similar dorsoventral compression, but differs in that the ventral rim is produced somewhat posteriorly. There is a thin film of calcified tissue on the inside of the cotyles and a narrow plug fills the notochordal canal medially. 2. *Hypapophyseal structures*.- The second cervical has a small, ventral flange under the anterior cotyle. Excepting this, a subcentral keel is lacking from the column. A ventral swelling is present on the rim of each anterior cotyle in the anterior portion of the trunk. In the posterior half this becomes small anterior basapophyses, which are lacking from the sacral and postsacral vertebrae. Subcentral foramina are absent.

The first haemal arch appears on the second caudosacral vertebra. The arch is simple, provided with a posteroventrally projecting spine, and lacks crests or other projections. In the more posterior part of the tail the haemal spine becomes bicipital.

3. *Neural arch*.- There is little variation in this part of the vertebra. The neural canal is large postcranially, but becomes smaller posteriorly. Spinal nerve foramina are lacking throughout the column.

4. *Neural crest and hyperapophysis*.- In the pectoral region, each vertebra possesses a well-developed, but low, neural crest, which is not quite raised to the level of the hyperapophysis. It extends much of the length of the roof of the neural arch. The crest decreases in height and length progressively until, on the sacrum, it is lacking. A small crest in the middle of the neural arch is re-developed in the caudal series.

The hyperapophyseal area is not well-developed, and the hyperapophysis is effectively lacking. This area is raised slightly and ends in a pair of ill-defined swellings. In the caudal vertebrae there is a bicipital hyperapophysis.

5. *Zygapophyses*.- Prezygapophyses in the pectoral region have facets developed as irregular ovals, positioned anterolaterally, and exhibiting

little or no lateral inclination. In the trunk proper the prezygapophyseal facets become significantly wider and they extend a greater distance anteriorly and laterally from the neural arch, trends that continue into the caudal vertebrae. Posterior to the pectoral girdle there is slight, but notable, lateral uptilt to the prezygapophyses. Postzygapophyses extend well back of the hyperapophyseal area. They are in the form of highly irregular circles and are smaller than the prezygapophyses with which they articulate.

6. *Transverse processes*.- The transverse processes are short, robust structures extending laterally and posteriorly from the vertebrae. The rib-bearers are confluent in T1, T2, and sacrum. The other trunk vertebrae, save the one or two immediately before the sacrum, have weakly, but distinctly, bicipital rib-bearers. The rib-bearers are not notably inclined from the vertical plane, with the dorsal and ventral arms being more or less one above the other.

The caudosacrals have elongate, unicipital transverse processes, which carry ribs. The first haemal vertebra also bears ribs. From here posteriorly the transverse processes decrease in size and length, also coming to extend more directly lateral.

ii) Family Cryptobranchidae Cope 1889

Cryptobranchus alleganiensis (Daudin 1803)

Specimens.- Two dry skeletons (UA 14326, 14327) and two cleared and stained specimens (UA 14413, 14414).

ATLAS. The anterior cotyles are irregular ovals, slightly wider than high, extending laterally on either side of the odontoid process, and situated largely below the neural canal. The surface of articulation is continuous over the anterior face of the odontoid process and merges laterally with the cotyles. In lateral view the cotyles are slightly tilted posterodorsally and are concave to flat. The odontoid process is a wide, robust projection extending relatively far anteriorly. It is grooved dorsally by the neural canal. In total, the anterior portion of the atlantal centrum resembles that of the fossil salamander *Scapherpeton*. The posterior cotyle is deeply concave, with some calcification internally. It tends to be subcircular in posterior view, with a thickened ventral rim. The chordal foramen is situated dorsally, just beneath the top of the centrum. There is sometimes a thick subcentral crest on the atlas.

The neural canal is a large, laterally compressed oval. In larger specimens the canal is smaller relative to the size of the atlas. A small flange of bone is present on the inner wall of each neural arch, just above the centrum. The roof of the arch extends dorsally into a relatively tall, thick neural crest, which is capped in cartilage. The neural arch is relatively robust, its walls rising almost straight dorsally, and slightly medially. The hyperapophyseal region is not developed. Spinal nerves exit intravertebrally through the walls of the neural arch, the passages continuing laterally through the anterior cotyles on either side.

There are no transverse processes.

SECOND CERVICAL (T1). The anterior cotyle is higher than wide, but this is accentuated owing to the dorsal position of the chordal foramen and the extension of the ventral border of the cotyle. The posterior cotyle is circular, with but a slightly thickened ventral rim. The centrum is deeply amphicoelous and there is a small amount of calcified tissue infilling the cotyles. A robust hypocentral keel joins the anterior and posterior cotyles. In some specimens, this keel is grooved on one side or the other by a blood vessel. There is no trace of basapophyses anteriorly. A variable number of subcentral foramina are found on either side of the keel.

The neural canal is wider than high, exhibiting a kidney shape in anterior view. There are no spinal nerve foramina. The neural crest is represented by a low ridge. The hyperapophysis is a large, slightly raised process, which is finished in cartilage. The walls of the neural arch are robust. Dorsally, between the prezygapophyses, the roof of the neural arch is notched. The prezygapophyses are heavy, projecting anterolaterally and dorsally from the front of the neural arch. They do not extend far beyond the front of the vertebra. The facets are irregularly shaped ovals or circles, with their axes extending anteriorly and slightly dorsally and laterally. The prezygapophyses are significantly larger than the postzygapophyses. The latter have relatively small, subcircular facets, which are tilted from the horizontal.

The transverse processes are long, robust, unicipital tubes extending laterally and slightly posteriorly. Medially, each transverse process is pierced by a large, longitudinal canal for a vertebral blood vessel. These canals cause a double joining of the transverse processes to the vertebra. Ventrally there is elongate attachment to the dorsal part of the centrum. In this position a small ventral lamella is formed in association with each transverse process. Dorsally the transverse processes originate mainly from the posterior quarter of the wall of the neural arch. In addition, there is a strut of bone extending anteriorly from these points, along the wall of the neural arch to the latter's anterior third.

TRUNK VERTEBRA (T9, see Fig. 3). The anterior cotyle is subcircular with the chordal foramen in a dorsal position. There is no infilling evident, but the walls of the centrum are thickened, especially ventrally. The posterior cotyle is somewhat teardrop-shaped and the ventral rim is produced posteriorly to a slight degree. The chordal foramen is located just beneath the floor of the neural arch. Basapophyses are lacking. There is a thick ridge joining the cotyles, but this does not drop below the level of the cotyles. Subcentral foramina are generally present, one on either side of the subcentral keel or a single one on one side or the other.

The neural canal is low and bean-shaped in anterior view. The roof of the neural arch is flat, rising gently posteriorly to the hyperapophysis. There are no foramina for the spinal nerves. The neural crest is represented by an indistinct ridge in the middle half of the roof. The hyperapophysis is a low, small bump finished in cartilage. No facets are developed, but musculature attaches to the ventral surface of the roof of the neural arch between the posterior zygapophyses. Prezygapophyseal facets are large elongate ovals, anterolaterally disposed and with the anterolateral edges raised dorsally. The postzygapophyseal facets are long and teardrop-shaped, extending anteroposteriorly and slightly posterolaterally. The posterior edges are turned down.

The transverse processes are long and robust, arising from the neural arch and dorsal part of the centrum just posterior to the midpoint of the vertebra. They incline posteriorly at about an angle of 120 degrees, and twist from the vertical such that the dorsal parts are further posterior than the ventral. The transverse processes are weakly bicipital, with the dorsal and ventral arms confluent. A small vertebrarterial canal pierces each process dorsal to the small ventral lamella and next to the centrum.

SACRUM (T19). The anterior cotyle is teardrop-shaped, but with the broadest part located ventrally. There is no infilling, the ventral rim of the cotyle is thickened, and the chordal foramen is dorsal. The posterior cotyle is subcircular, but somewhat wider than high. The ventral rim is thickened and produced slightly posteriorly. There is no infilling and the chordal foramen is dorsal. Basapophyses and a hypapophysis are lacking and there are subcentral foramina.

The neural canal is low and wide. The roof of the neural arch is flat and the walls lack foramina for spinal nerves. A small, but distinct, neural crest is present in the middle half of the roof. The hyperapophysis is a small boss on the posterior of the neural arch, raised slightly above the level of the roof of the arch. Facets are lacking from the hyperapophysis. The prezygapophyseal facets are developed as in the trunk vertebra described. Postzygapophyseal facets are small ovals, more or less in the horizontal plane and laterally extending.

The transverse processes are large and robust. They are distinctly bicipital, but the cavities at the expanded distal ends are confluent.

The transverse processes originate just posterior of the middle part of the vertebra and angle posteriorly at about 120 degrees, at least in larger individuals. The rib-bearers are in a single vertical plane and ventral lamellae are present, although the posterior alar processes are small. Vertebrarterial foramina are very large.

HAEMAL VERTEBRA (H3). Both anterior and posterior cotyles are subcircular with robust rims. Infilling is lacking, there are no flanges developed on the rims, and the chordal foramen is in a dorsal position. A large haemal canal is present below the centrum. Only the posterior part of the centrum bears the haemal arch. From this arch a long, dorsoventrally flattened, haemal process projects posteroventrally. The process bears a small median ridge on its ventral surface.

The neural canal is large, and the roof of the neural arch is slightly domed above. There are no foramina for the exit of spinal nerves. The neural crest is a low, sharp ridge beginning behind the prezygapophyses and running posteriorly to the tip of the hyperapophysis. The latter is a long, thick tube extending posterodorsally from the neural arch. Postzygapophyseal facets are small ovals on the ventrolateral edges of the hyperapophysis. Prezygapophyseal facets are anterolaterally placed ovals with the lateral borders strongly tipped dorsally.

Transverse processes on the third haemal vertebra are well-developed, but short. They are generally unicipital with dorsal flanges of bone, but they may be divergently bicipital. The transverse processes originate midvertebrally and are strongly posteriorly inclined. Alar processes are variably developed, but a system of dorsal, ventral, anterior, and posterior alars is often present. A minute vertebrarterial canal is present.

VARIATION ALONG THE COLUMN. *1. Cotyles*.- The anterior cotyle tends to be circular throughout the column, with the more anterior vertebrae having a cotyle somewhat higher than wide. The posterior cotyle is in the shape of a broad teardrop, this being especially marked in the second cervical (T1). In the most posterior trunk vertebrae and in the sacral, the posterior cotyle is teardrop-shaped but with the broadest part ventral, reversing the shape found more anteriorly.

Postsacrally, anterior and posterior cotyles are approximately circular. Infilling of the cotyles by calcified tissue is not evident anywhere along the column. However, the rims of the cotyles are thickened and the ventral rim of the posterior cotyle projects a short distance posteriorly in the trunk vertebrae.

2. *Hypapophyseal structures*.- All vertebrae except for the atlas and the sacral generally have hypapophyseal structures. Basapophyses are absent throughout the column. In the trunk series, the hypapophyseal keel is robust, concave dorsally in lateral view, and does not extend beneath the level of the cotyles. In the first postsacral vertebra, these paired structures each give rise to a posterior rod. These rods extend posteroventrally, converge, and are joined by a web of bone distally. Posteriorly, the haemapophysis thus formed becomes more arch-like, the haemal canal smaller, and a haemal process develops. The haemal process is a long, posteroventrally directed rod, subequal in size and orientation to the hyperapophysis of the neural arch.

3. *Neural arch*.- The neural arch is a low, robust structure throughout the column posterior to the first few vertebrae. There are no foramina for spinal nerves except in the atlas.

4. *Neural crest and hyperapophysis*.- A tall robust neural crest is present on the atlas, capped in cartilage even in large individuals. A low median swelling of the neural arch in the trunk region might be interpreted as a neural crest, but it is probably more accurate to describe the crest as absent. The neural arch rises posteriorly from the midpoint of the roof. At the posteromedian edge it gives rise to a small, low protuberance — the hyperapophysis. The height of the latter is greatest in the anterior part of the column and decreases posteriorly to a minimum immediately presacrally. In the postsacral vertebrae the hyperapophysis becomes progressively longer. In the haemal series it is an elongate rod extending posteriorly over the next posterior vertebra.

5. *Zygapophyses*.- The prezygapophyseal facets extend anteriorly and laterally from the front of the neural arch. In the anterior part of the trunk the facets are oval to teardrop-shaped, whereas posteriorly they are more elongate, but then shorten again immediately presacrally. The lateral borders of the facets are tilted dorsally. In the caudal vertebrae there is progressively more inclination until the facets are vertical.

The postzygapophyseal facets are teardrop-shaped in the anterior region of the trunk. They are progressively more oval posteriorly and finally are irregular circles in the five or six vertebrae in front of the sacrum. The placement of the facets is primarily anteroposterior, but with a small posterolateral component. The posterior zygapophyses of the postsacral vertebrae are reduced until, in the haemal series, they are tiny facets on the ventrolateral edges of the hyperapophysis.

6. *Transverse processes.*- Transverse processes are lacking from the atlas. The second cervical has long, robust unicipital processes, which extend posteriorly at about 105 degrees. The transverse processes of the trunk vertebrae are weakly bicipital, the arms being closely appressed and confluent. In the more anterior region the dorsal and ventral arms are in a single vertical plane. More posteriorly, the transverse processes become inclined, the ventral arms further anterior than are the dorsal. In the sacrum the arms once again lie vertically.

Ventral lamellae are well-developed throughout most of the column. The first and second haemal vertebrae have small ventral lamellae, but these are lacking posteriorly. Transverse processes are present on the more anterior haemal vertebrae, becoming gradually reduced posteriorly, and disappearing from the sixth or seventh haemal vertebra. Large vertebrarterial canals are present, located just above the ventral lamellae next to the centrum.

iii) Family Amphiumidae Gray 1825

Amphiuma tridactylium Cuvier 1827

Specimens.- One dry skeleton (UA 14364).

ATLAS. The anterior cotyles are large irregular hemispheres, with straight medial borders next to the neural canal and odontoid process. The dorsal and ventral borders of each cotyle extend slightly forward, leaving a central depression. The cotyles extend about halfway up the sides of the neural canal. In lateral view they are in the vertical plane. The odontoid process is large and elongate, with a median groove and large ventrolateral articular facets, which join with the occipital condyles of the skull. The posterior cotyle is large and has a substantial amount of calcified tissue infilling, producing a shallow cavity. The cotyle is elongate and laterally compressed, with the ventral half projecting posteriorly. The chordal foramen is small and located far dorsally. Basapophyses and hypapophysis are lacking.

The neural canal is small, irregularly oval in anterior view, and slightly pinched ventrally by the anterior cotyles. The sides of the neural arch are robust, arising from the posterodorsal edges of the anterior cotyles. Very small foramina pierce the neural arch where the latter joins the anterior cotyles. The neural crest is a thick, low ridge extending the length of the roof of the neural arch and then rising posteriorly with the hyperapophysis. There are two small lateral accessory ridges running the length of the roof. Posteriorly the roof of the neural arch rises steeply into a tall, robust hyperapophysis, which has posteriorly directed, vertical facets. The postzygapophyseal facets are teardrop-shaped, posterolaterally oriented, and with the edges slightly raised. In the available skeleton, the left zygapophysis is anomalous owing to extra deposition of bone between it and the neural arch.

Transverse processes are not developed.

SECOND CERVICAL (T1). The anterior cotyle is small, in the shape of an elongate teardrop, and has a thick boss of bone extending from the ventral border. There is a large amount of infilling, the cotyle being extremely shallow, and an irregular plug obliterates the chordal foramen. The posterior cotyle is subcircular, the vertical diameter exceeding the horizontal. The ventral rim is excavated anteriorly and there is a large amount of uniform infilling, with the chordal foramen being a small, dorsal opening. The subcentral keel is robust with a straight ventral border produced well below the cotyles. There is an irregular mass of bone beneath the cotyle, but anterior basapophyses are not differentiated.

The neural canal is low and wide, its roof flattened. Spinal nerve foramina are absent. The neural spine is tall, rising well above the level of the hyperapophysis and occupying the posterior half of the roof of the neural arch. The hyperapophysis is composed of lateral flanges from the posterior border of the neural crest extending over the postzygapophyses. There are two vertical, posteriorly facing facets on the hyperapophysis. Prezygapophyseal facets are anteroposteriorly extended ovals of irregular shape, correlating with the anomalous development of the postzygapophyses of the atlas. Postzygapophyseal facets are elongate ovals running posterolaterally and with the lateral edges strongly uptilted.

Transverse processes are very long and slender. The left one is unicipital, the right has a small ventral accessory facet making it weakly bicipital. The transverse processes originate from just posterior of the midpoint of the vertebra and extend posterolaterally. Small alar processes are present posteriorly and the vertebrarterial canals are narrow and long.

TRUNK VERTEBRA (T27, see Fig. 4). The anterior cotyle is large and subcircular, with a central chordal foramen. There is extensive infilling, so as to produce a uniform, shallow depression. The posterior cotyle is teardrop-shaped, with a dorsal chordal foramen and much infilling. The ventral borders of both cotyles are slightly extended. The hypapophysis is a robust keel extending from cotyle to cotyle. It is concave upwards in lateral view and drops slightly below the level of the posterior cotyle. Two irregular subcentral foramina are present. Two lateral ridges extend from the anterior part of the subcentral keel along the cotyle and proceed ventrally and anteriorly as anterior basapophyses.

The neural canal is small and low, with a sloping roof. Spinal foramina are lacking. The neural crest is tall and thin, rising vertically from the posterior edge of the prezygapophyseal facets and then proceeding horizontally to meet the top of the hyperapophysis. The hyperapophysis is composed of two lateral flanges paralleling the posterior border of the neural crest. It accommodates two posteriorly facing facets. The prezygapophyseal facets are large irregular ovals, almost rectangular in outline. They extend almost straight laterally, but with a slight anterolateral component. The lateral edges are slightly tilted upwards. The postzygapophyseal facets are broad teardrops with a posterolateral extension. The lateral edges are inclined downwards. From the surface of each posterior zygapophysis a thick, low ridge extends anteriorly and medially to terminate on the roof of the neural arch at the level of the front of the neural crest. This zygapophyseal crest serves as a site of attachment for a myoseptum of the *dorsalis trunci* (see descriptions below).

Transverse processes are long, thin, and unicipital, originating on the dorsal part of the centrum about midcentrally. They extend gently posteroventrally. Small first alar processes are present, and well-developed second alar processes arise from the anterior surfaces of the transverse processes and the lateral walls of the centrum. Distally, the second alar processes are produced into blunt points, which correlate with anterior flexures in the trunk musculature (see descriptions below). A small ridge occupies the anterodorsal surface of each transverse process, corresponding to the third alar process of *Siren* (see Fig. 1).

SACRUM. There is no sacral vertebra, even though there is a pelvic girdle.

HAEMAL VERTEBRA (H2). Both anterior and posterior cotyles are circular, with a small amount of uniform infilling, and the chordal foramen is located dorsally. A complete haemal arch does not appear until the seventh haemal vertebra. In the more anterior haemals a pair of hypapophyses arises along the lateral edges of the centrum. They angle posteriorly, narrowing to end in blunt points. The processes diverge slightly from each other and the arch is incomplete. In the seventh haemal the diverging processes are joined distally by a flat piece of bone.

The neural canal is low, with the roof gently rounded. Spinal nerve foramina are absent, but appear in the more posterior haemal vertebrae (see Edwards 1976). There is a low, triangular neural crest occupying the middle half of the roof of the neural arch. The hyperapophysis is composed of two diverging processes extending posterodorsally above and beyond the postzygapophyses. The posteroventral surface of the hyperapophysis is flattened and facets are lacking. Prezygapophyseal facets are laterally extending ovals, slightly dorsally inclined on the outer edges. Postzygapophyseal facets are irregular ovals, extending posterolaterally, with the lateral edges tilted dorsally.

Transverse processes are small, unicipital, and lateroventrally directed. They are composed of three alar processes, the first and second combining to form ventral lamellae and a vertical dorsal alar (the third) joining with the neural arch and prezygapophysis. Transverse processes arise from the anterior part of the centrum and lack vertebrarterial canals.

VARIATION ALONG THE COLUMN. *1. Cotyles.*- The cotyles are of relatively constant shape along the column. In the trunk series the anterior cotyle is a vertically elongate oval, whereas the posterior cotyle is teardrop-shaped. In the cloacal region, cotyles are dorsoventrally flattened and in the haemal series they are circular. Throughout the column the cotyles are partially filled with calcified tissue, producing a shallowly amphicoelous centrum (see also Fig. 93). A distinct chordal foramen is usually present, but one or two vertebra have the foramen obliterated by a plug of calcified tissue. When adjacent vertebrae are broken apart in a dry skeleton, the notochordal tissue between the cotyles is in the shape of a sphere, not the sharp cone seen in *Necturus*, for example.

2. Hypapophyseal structures.- The hypapophysis is lacking from the atlas. On the next three vertebrae the hypapophyseal keel is well-developed, produced ventrally beneath the ventral borders of the cotyles. Posteriorly, as the basapophyses become well-developed, the hypapophysis comes to project slightly below the posterior cotyle. This association of basapophyses and posterior hypapophyseal projection recalls the condition of *Desmognathus* (q.v.).

In the posterior trunk region the hypapophysis is gradually reduced, finally disappearing in the cloacal and pre-haemal vertebrae. In many trunk vertebrae the blood vessels exiting through the subcentral foramina cause the formation of a vertical groove on either side of the hypapophysis. In the haemal vertebrae a paired hypapophysis is present, composed of two large, posterolaterally directed processes. Further back these are joined by a web of bone, forming the haemal arch proper. The haemal arch has complex ridges, coming to mirror the neural arch and its associated structures.

Basapophyses are lacking on the first and second trunk vertebrae, the three vertebrae immediately anterior to the haemal series, and from all haemal vertebrae. They are relatively constant along the column, remaining large and well-developed so long as they are present. They are anteriorly situated and project anteroventrally beneath the anterior cotyle.

3. *Neural crest and hyperapophysis*.- Neural crests and hyperapophyses are present throughout the column until the terminal caudal region. On the atlas the neural crest is a broad, low ridge, but in the following vertebrae it is a tall, thin crest. In the more anterior trunk vertebrae the crest occupies the posterior half of the roof of the neural arch. In the succeeding vertebrae the anterior edge shifts forward to stabilize its origin slightly behind the anterior border of the neural arch. In the pectoral region the neural crest rises well above the level of the hyperapophysis. However, this height is reduced posteriorly and along most of the trunk the neural crest and hyperapophysis are subequal in height. In the postcloacal and haemal vertebrae there is progressive

lowering of the posterior part of the neural crest, and it eventually becomes a small midvertebral flange.

The hyperapophysis rises nearly vertically from between the postzygapophyses. It joins to the rear of the neural crest as a pair of laterally directed flanges, producing two posteriorly facing, vertical facets between the postzygapophyses. In dorsal view the neural crest and hyperapophysis of each vertebra produce a T-shaped structure. The development of the hyperapophysis is constant along the column until the cloacal and haemal vertebrae, in which it is composed of a pair of diverging, posterodorsally projecting spines. In these, posterior facets are lacking. The posterior facets serve as areas of insertion for the hyperapophyseal muscles.

4. *Zygapophyses*.- In most vertebrae the prezygapophyseal facets extend laterally and slightly anteriorly. Their lateral edges are tilted dorsally. Postzygapophyseal facets extend posterolaterally, their outer edges dipping slightly downward. The facets are shallowly concave upwards. In the more posterior haemal vertebrae the prezygapophyses shift position until they orient anteroposteriorly, with the lateral borders raised dorsally. The associated postzygapophysis show analogous changes to accommodate the prezygapophyses. In the most posterior caudal vertebrae (the last five to ten) zygapophyses disappear.

5. *Transverse processes*.- There are no transverse processes on the atlas. The second cervical bears well-developed, bicipital transverse processes with the rib-bearers closely appressed. The transverse processes are angled posteriorly at about 110 degrees. Alar processes are lacking and the arms are situated in a single vertical plane. T2 has

bicipital transverse processes, with the rib-bearers closely appressed. These extend posterolaterally at a slightly greater angle than those of T1. Posteriorly, the second alar processes increase in size, but first alar processes remain small. After T2 the transverse processes are unicipital and come to lie at right angles to the centrum. In the cloacal region, the second alar processes are gradually reduced. In the caudal series the first alar processes become subequal to the second and the transverse processes are horizontal plates, which extend from the anterior half of the centrum. Only the most posterior caudals lack transverse processes completely.

iv) Family Ambystomatidae Hallowell 1857

Ambystoma tiheni Holman 1968

Specimens.- The only two known trunk vertebrae, SMNH 1431 (holotype), and SMNH 1432 (paratype), from the lower Oligocene of the Cypress Hills, Saskatchewan.

DESCRIPTION (see Fig. 5). The anterior cotyle is, apparently, subcircular in outline. Insofar as can be determined (there is wear and breakage) the posterior cotyle is also subcircular. There is what appears to be significant infilling of the anterior cotyle by calcified tissue, causing the cotyle to be relatively shallow. There are no basapophyses or hypapophyses and subcentral foramina are lacking.

The neural canal is wider than high and dorsoventrally flattened. Relative to the centrum, the neural arch is massive and greatly expanded laterally. The roof of the arch is slightly arched medially, and wide. The neural crest runs almost the entire length of the arch, but is low, being merely a small ridge. The spinal nerve foramina are located at the base of each transverse process, between the two rib-bearers. The foramina open almost straight backwards.

The prezygapophyses are large elongated ovals, raised laterally and extended anteriorly and slightly laterally. Postzygapophyses are worn, but appear to have been relatively small ovals. The hyperapophysis is low. It extends posteriorly to just beyond the posterior zygapophyses, ending bicipitally in finished bone.

Transverse processes are extremely robust, elongated rods extending laterally and slightly posteriorly. The dorsal rib-bearers are just posterior of the ventral. The rib-bearers are divergent and joined by a web of bone for almost their entire lengths. They are expanded distally. The very large size and distal expansion of the transverse processes could be taken as indicating that the two specimens are sacral vertebrae. Against this are the following:

1) the relatively great length of the transverse processes;
2) the relatively small foramina for the spinal nerves (usually enlarged in the sacrum); and
3) both vertebrae have the same enlarged transverse processes.

The point of attachment of the ventral rib-bearer to the centrum and neural arch is massive. Therefore, in conjunction with the massive neural arch, there is a flattened surface on either side of the midportion of the centrum.

DISCUSSION. Holman (1968) held that this species was related to the *Ambystoma opacum* group of Tihen (1958) on the basis of size and proportions. However, *Ambystoma tiheni* differs in having the neural arch more depressed, in "obsolete" subcentral foramina, in having the ends of the centrum less widely flared, and in that the transverse processes are much more robust (see Holman 1968). There is not a special, or even vague, resemblance to *A. opacum* or *A. talpoideum*, from which *A. tiheni* also differs in the form of the hyperapophysis, zygapophyses, and neural crest. Association of these species in the same species group is probably unwarranted.

Owing to the presence of foramina for the spinal nerves, *A. tiheni* cannot be a hynobiid, although there are several other resemblances. It resembles *A. maculatum* in the structure of the hyperapophysis. Surprisingly, there are several resemblances to vertebrae of *Plethodon*, although those of the latter are more delicate. The overshadowing of the centrum by the laterally expanded neural arch, the elongation and primarily anteroposterior extension of the prezygapophyses, and the bicipital endings of the hyperapophysis are all features shared with *Plethodon*. The major difference is in the robust nature of the vertebra and in the large transverse processes, which are of small diameter and short in *Plethodon*.

The fossil vertebrae show no special resemblance to any extant salamander and it is quite possible that they do not belong in the genus *Ambystoma*. Nevertheless, pending the discovery of further material, they are best retained in *Ambyostoma* and they may prove to be related to *A. macrodactylum* and *A. gracile*.

Ambystoma gracile (Baird 1859)

Specimens.- One skeletonized adult (UA 14329) and one cleared and stained larva (UA 14418).

ATLAS. The anterior cotyles are subcircular, but with flattened edges dorsomedially where they abut the neural canal. The articular surfaces are relatively flat, but they extend anteriorly onto the edge of the odontoid process and angle slightly posteriorly ventral to the odontoid. Each cotyle slopes posterodorsally, and is situated largely below the level of the neural canal. Each is pierced by a relatively large foramen for the spinal nerve. The odontoid process is wide, relatively short, and thin dorsoventrally. It extends anteroventrally from between the anterior cotyles, rather than straight forward as in the majority of salamanders. There is a wide groove dorsally.

The posterior cotyle is an irregularly shaped circle with the ventral half narrower than the dorsal. The chordal foramen is wide and slightly above the centre of the cotyle. There is considerable infilling by calcified tissue, but the cotyle is deeply concave. The ventral surface of the atlas is Y-shaped, with the two anterior cotyles forming the arms and the centrum the stem. Hypapophyseal structures are lacking except for a pair of faint posterior basapophyses.

The neural canal is large and subcircular in anterior view. There is a raised, roughened boss on the anterior part of the roof of the neural arch. The neural arch extends somewhat forward over the anterior cotyles. A faint ridge runs posteriorly to connect the anterior boss to the hyperapophysis. The tip of the latter structure is finished in cartilage. Two well-separated, posteriorly facing facets form the hind border of the hyperapophysis. Postzygapophyses are small ventral appendages of the hyperapophysis and roof of the neural arch. The facets are approximately teardrop-shaped, but with flattened posterior borders. The lateral edges are tilted dorsally.

There is no trace of transverse processes.

SECOND CERVICAL (T1). The centrum is small relative to the neural arch. The anterior cotyle is subcircular, the chordal foramen more or less central, and there is a notable amount of irregular calcification within the deep cotyle. The dorsal border of the anterior cotyle is further forward than is the ventral. The posterior cotyle is dorsoventrally compressed with the ventral border somewhat posterior of the dorsal. Otherwise it is as the anterior cotyle. Elongate posterior basapophyses are present. These diverge posteriorly from the middle of the centrum, extending to the edge of the posterior cotyle. Midcentrally a narrow low subcentral keel is present, continuous with the posterior basapophyses. Small subcentral foramina are present.

The neural canal is large. In anterior view the walls of the arch extend dorsolaterally and the roof is gently curved dorsally. A small foramen pierces the wall of the neural arch anterior to each transverse process. There is no trace of a neural crest, the neural arch being smooth. The hyperapophysis rises slightly dorsally and is wide, finished in irregular bone and cartilage. A pair of distinct facets rise dorsomedially from the upper surfaces of the postzygapophyses. The anterior zygapophyses are forward extensions of the neural arch, and provided with facets in the shape of anteroposteriorly elongate ovals. Their disposition is anterior and very slightly lateral. The lateral borders are raised. Postzygapophyses are developed as those of the atlas.

Transverse processes are short and robust. The dorsal rib-bearers are larger than the ventral, to which they connect by a web of bone.

Both rib-bearers extend posterolaterally and are tilted posterodorsally in lateral view. The ventral rib-bearers have a wide connection with the centrum, forming small, but thick, alar processes. The dorsal rib-bearers originate on the posterior third of the walls of the neural arch. The rib-bearers diverge to a slight degree. A small vertebrarterial canal pierces each ventral rib-bearer.

TRUNK VERTEBRA (T9, see Fig. 7). The anterior cotyle is subcircular, but with the lateral diameter somewhat greater than the dorsoventral. The dorsal rim extends a short distance anteriorly. The posterior cotyle is of similar shape, but with the ventral rim extending posteriorly. In both, the chordal foramen is slightly dorsal in position and there is irregular infilling by calcified tissue. A hypapophyseal keel is lacking, but anterior basapophyses are present as very faint ridges on the lateral edges of the centrum.

The neural canal is wide and flattened, being of a depressed kidney shape in anterior view. The spinal nerve foramina pierce the neural arch just posterior to the origin of the ventral rib-bearers. There is no neural crest, although the roof of the neural canal is somewhat arched. The hyperapophysis is a low, hollow, short, and wide spine.

Prezygapophyses extend forward from the anterodorsal edges of the neural arch. The facets are large, elongate teardrops that are sometimes truncated anteriorly. These facets are raised laterally. Postzygapophyses are somewhat smaller than the prezygapophyses, but are otherwise reverse images of the latter.

Transverse processes are short and small, extending posterolaterally. The rib-bearers are bicipital, but nondivergent, closely appressed, and separated by narrow webs of bone. The ventral rib-bearers arise from the dorsal part of the midcentrum and are partially incorporated into the walls of the neural arch. The smaller dorsal arms extend more sharply posteriorly from the posterior half of the neural arch, such that they are behind the ventral arms distally. The ventral rib-bearers are pierced by small vertebrarterial canals. Alar processes and subcentral foramina are lacking.

SACRUM (T15). The structure of the sacrum is very like that of the trunk vertebrae, differing primarily in hypertrophy of the transverse processes. Anterior and posterior cotyles are as in the trunk vertebrae. The subcentral keel and anterior basapophyses are absent and a small subcentral foramen pierces the ventral rib-bearer on either side of the centrum.

The neural canal is low and wide, but expanded over those of the preceding vertebrae. A large nerve foramen pierces the neural arch behind each transverse process. The neural crest is absent and the hyperapophysis is low, robust, and short. Anterior and posterior zygapophyses are developed as in the trunk, although the latter are proportionally smaller than in the presacrals.

Transverse processes originate from the neural arch dorsal to the midpoint of the centrum. They are bicipital, but appressed and confluent. The dorsal arms are larger than the ventral and diverge somewhat from them. The distal tips of the rib-bearers are in a single horizontal plane. A very small vertebrarterial canal pierces each transverse process ventrally near to its origin from the vertebra.

HAEMAL VERTEBRA (H3). The anterior cotyle is dorsoventrally compressed and the posterior is circular. The centrum is deeply amphicoelous with a small amount of calcified infilling and the plugged chordal foramen is located centrally. The haemal arch is fully developed, covering much of the ventral border of the centrum, but there is a deep V-shaped notch anteriorly. The haemal canal is narrower and higher than the neural canal. A pair of foramina, one significantly larger than the other, pierce the haemal arch, one on either side. The haemal process is robust and extends posteriorly a greater distance than does the hyperapophysis of the same vertebra.

The neural canal is small, low, and wide. The roof of the neural canal is flat. A small foramen for the spinal nerve pierces the arch immediately posterior to each transverse process. There is no neural crest, although the roof is gently domed medially. The hyperapophysis is large and robust, extending posterodorsally as a hollow rod. It is relatively longer than those of the trunk vertebrae and tipped in cartilage. Posterior facets are not evident. The prezygapophyses extend anterolaterally a short distance beyond the neural arch. The facets are broad irregular teardrops, extended anterolaterally and with a minimal amount of dorsolateral inclination. Postzygapophyses are smaller irregular teardrops that extend posterolaterally. They are small lateral outgrowths from the neural arch and buttressed to the hyperapophysis by a small web of bone.

Transverse processes are short and unicipital, but well-formed. They extend laterally and slightly posteroventrally from the midpoint of the wall of the neural arch.

VARIATION ALONG THE COLUMN. 1. *Cotyles*.- The anterior cotyle is deeply concave throughout the column, with the chordal foramen more or less centrally located. The vertebrae in association with the pectoral girdle (T2, T3, and T4) have a dorsoventrally compressed anterior cotyle, as do the caudosacrals and the majority of the haemal vertebrae. The remainder of the anterior cotyles are subcircular. The first two trunk vertebrae, the presacrals, sacral, and caudosacrals have the dorsal rim of the anterior cotyle extending somewhat further forward than the ventral.

The posterior cotyle is also deeply concave with irregular infilling. That of the atlas, T1-3, the presacrals, the sacrals, and the caudosacrals is a dorsoventrally compressed oval. The majority of the trunk vertebrae have a subcircular posterior cotyle, while that of the haemal series is variable. Throughout the column the ventral rim of the posterior cotyle extends posteriorly to a small degree.

2. *Hypapophyseal structures*.- Elongate, posteriorly diverging posterior basapophyses are present on the atlas, T1 and T2. These become progressively more strongly developed in T1 and T2. Other trunk vertebrae, excepting a few in the middle of the trunk, which have elongate anterior basapophyseal ridges, lack basapophyses. A large larva (UA 14418), possibly a neotene, has well-developed, although low, posterior basapophyses on the atlas and T1 through T3. All of the following trunk vertebrae, up to and including the sacrum, have well-developed anterior

basapophyses. Subcentral keels are not present on any of the vertebrae.

The first haemal vertebra (the third caudosacral) bears a complete and well-developed haemal arch. In the adult specimen (UA 14329), the second haemal vertebra lacks a haemal arch, but has a pair of ridges present ventrolaterally on the centrum. The haemal spine curves gently posteroventrally from the arch to a greater distance than the hyperapophysis of the same vertebra. The haemal spine decreases in size posteriorly, correlated with the decrease in size of the caudal vertebrae. The haemal arch arises along the entire ventrolateral edges of the centra, except for a small gap anteriorly and (sometimes) posteriorly.

3. *Neural crest and hyperapophysis*.- But for the anterior boss on the atlas, a neural crest proper is lacking from the vertebrae. The hyperapophysis is low, robust, and unicipital, extending only to the posterior border of the postzygapophyses in the trunk region. That on the sacrum, caudosacrals, and haemals extends a greater distance posteriorly. That of the haemal vertebrae extends posterodorsally at a greater angle. Facets are present on the posteroventral surface of the hyperapophysis in the atlas and T1 to T3 or T4. The hyperapophysis ends in irregularly calcified tissue or cartilage.

4. *Zygapophyses*.- The prezygapophyseal facets of the second cervical are small, laterally upturned elongated teardrops. They are only slightly displaced anterolaterally from the anteroposterior plane. From here posteriorly until the middle of the trunk the following changes occur: the prezygapophyses become less dorsolaterally tilted, the facets increase in size (those of T8 being about two times those of T1), and the facets become slightly more anterolaterally oriented. From the midtrunk region

posteriorly the facets are almost horizontal, extended slightly anterolaterally, and undergo minor decrease in size. This decrease continues posteriorly throughout the caudal series. The prezygapophyses of the haemal vertebrae become foreshortened anteroposteriorly and, in contrast to those of the preceding vertebrae, only extend a very short distance beyond the neural arch. All prezygapophyses extend dorsolaterally from the top of the neural arch.

The posterior zygapophyses reflect the changes in the prezygapophyses.

5. *Transverse processes*.- Moving posteriorly from T1, the rib-bearers become progressively smaller in diameter. Up to T7 or T8 the rib-bearers are relatively divergent; however, from this point on they remain bicipital but are relatively closely appressed. T7 and T8 are anomalous in the available skeleton, the former having a unicipital transverse process on the left and a tricipital one on the right. T8 has a normally bicipital left transverse process and a unicipital right. From T8 posteriorly the ventral rib-bearers are markedly larger than the dorsal. Finally, the first three presacrals possess unicipital transverse processes. The two caudosacrals have relatively long, laterally extending, unicipital transverse processes. From here posteriorly the transverse processes are progressively reduced, with the fourth haemal lacking all traces.

Alar processes are lacking throughout the column, although, especially in the immedately postatlantal vertebrae, the ventral rib-bearers may be proximally dilated. Subcentral foramina are generally lacking. If present they are minute holes on one side or the other of the centrum, piercing the ventral rib-bearer. This lack presumably correlates with the lack of ventral lamellae.

Ambystoma maculatum (Shaw 1802)

Specimens.- Two skeletons (UA 14330, 14331) and two cleared and stained specimens (UA 14420, 14421).

ATLAS. The anterior cotyles are approximately circular, but of somewhat greater diameter vertically than horizontally. In lateral view they are in the vertical plane, with the ventrolateral borders thrust forward. The cotyles are widely separated by a short, robust odontoid process, which bears part of the cotylar facets laterally. The posterior cotyle is subcircular, with the ventral border extending posteriorly. There is a small amount of uniform infilling and the chordal foramen is dorsal. The centrum is long in comparison to other *Ambystoma*. Posterior basapophyses are thick, low lateral ridges on the centrum posterior to the anterior cotyles.

The neural canal is large and subcircular. The arch is a long, robust structure, its sides rising dorsomedially and uniting to form a tall, wide neural crest. On either side of the neural crest is a ridge that runs anteroposteriorly, to flare into lateral flanges anteriorly. The hyperapophysis rises as an inverted V over the postzygapophyses. The rear face of the hyperapophysis bears a pair of facets extending dorsomedially from the tops of the postzygapophyses. The zygapophyseal facets are small, elongate ovals, disposed anteroposteriorly and more or less horizontally.

Atlantal transverse processes are present, but small and ribless. They are posterolaterally directed flanges extending from the ventral part of the centrum and the neural arch to enclose a posteriorly facing concavity. There are no vertebrarterial canals.

SECOND CERVICAL (T1). The anterior cotyle is oval with the long axis vertical. There is a large amount of calcified tissue infilling the cotyle, producing a shallow concavity. The chordal foramen is central and the dorsal rim extends forward. The posterior cotyle is also oval, with much infilling, but the concavity is deeper. The cotylar rim is produced ventrally and the chordal foramen is wide and dorsal. A hypapophysis is represented by a low, median bump on the anterior cotyle. A pair of low, elongate posterior basapophyses is present.

The neural canal is relatively high with the roof rounded. There are no foramina for the spinal nerves. The neural crest is high and thick, extending from the front of the neural arch to unite with the hyperapophysis. The hyperapophysis is high and ends bicipitally, completely finished in bone. The posterior surface bears a pair of narrow, vertical facets. Prezygapophyseal facets are oval, extended anteroposteriorly and slightly anterolaterally. They are more or less horizontal. Postzygapophyseal facets are teardrop-shaped, extend anteroposteriorly, and orient horizontally.

Transverse processes are relatively long and robust, with closely appressed rib-bearers. The ventral arms originate just in front of the middle of the centrum, the dorsal from the middle of the neural arch. They angle posteriorly and are in a single vertical plane distally. There are no alar processes and relatively large vertebrarterial canals are present.

TRUNK VERTEBRA (T8, see Fig. 6). The anterior cotyle is subcircular with the ventral edge produced anteriorly and somewhat flattened. There is some infilling, but the cotyle retains a deep concavity and a dorsal chordal foramen is present. The posterior cotyle is subcircular with infilling; a ventral, posteriorly produced flange and a dorsal chordal foramen are present. Hypapophysis and basapophyses are absent.

The neural canal is flat and wide, being bean-shaped in anterior view. A small foramen for the spinal nerve is located just behind the dorsal arm of the transverse process on either side. The neural crest is thin and relatively high for an ambystomatid, beginning one third of the way behind the front of the neural arch. Its anterior face rises steeply and then continues horizontally to meet the hyperapophysis. This latter ends in two lateral processes and bears two posterior facets, each rising dorsomedially from a posterior zygapophysis. The prezygapophyseal facets are elongate ovals or teardrops, extending mainly anteroposteriorly and with the outer edges raised. Postzygapophyses have elongate, teardrop-shaped facets, which extend anteroposteriorly with the lateral edges upturned.

The transverse processes are quite long and thin, bicipital but closely appressed. The tubes forming the rib-bearers are filled with calcified cartilage. The transverse processes originate midvertebrally and are strongly swept posteriorly. They are slightly tilted from the vertical, such that the ventral arms are anterior of the dorsal. Alar processes are absent and the vertebrarterial canals are small.

SACRUM. The sixteenth trunk vertebra is usually the sacral. It is similar to the trunk vertebrae except as regards the large transverse processes.

Anterior and posterior cotyles are subcircular with some dorsoventral flattening. There is a small amount of infilling and the chordal foramen is situated dorsally. The ventral rim of the posterior cotyle is produced slightly posteriorly. Hypapophyseal keel and basapophyses are absent. Small subcentral foramina are present.

The neural canal is low, but not depressed, and wide. A large foramen for the spinal nerve is present just behind each transverse process. The roof of the neural arch is flat with a thin, medium-sized neural crest in the middle three quarters. The hyperapophysis is low, ending just behind the postzygapophyses in two robust prongs. There are two median facets facing posteroventrally. Prezygapophyseal facets are broad ovals, extending anterolaterally with the lateral edges raised slightly. Postzygapophyseal facets are subcircular and situated anteroposteriorly and somewhat posterolaterally. In rear view the facets are low internally and raised externally.

Transverse processes are long and angled gently posteriorly. Dorsal and ventral arms have the distal ends expanded and lying in a single vertical plane. The transverse processes are bicipital, but the arms are nondivergent and appressed. There are no alar processes and vertebrarterial foramina are small.

HAEMAL VERTEBRA (H3). Anterior and posterior cotyles are circular. In the anterior there is a significant amount of infilling to produce an internal rim, pierced by a large, central chordal foramen. The posterior cotyle has a small amount of uniform infilling and the ventral border is produced posteroventrally. The chordal foramen is dorsally located. The haemal arch covers the posterior two thirds of the centrum, surrounding a large haemal canal. The haemal crest is small, and the haemal process ends bicipitally in two robust, diverging points.

The neural canal is low, with an arched roof. A small spinal foramen is located just behind the dorsal arm of each transverse process. A low, thin neural crest occupies the posterior two thirds of the roof of the arch, running up the hyperapophysis. The latter is low and bicipital, ending in robust points, which extend behind the posterior zygapophyses. The posterior surface bears two small medial facets. Prezygapophyseal facets are oval, extended anterolaterally, and oriented more or less horizontally. They are situated well below the level of the roof of the neural arch. Postzygapophyseal facets are oval- to teardrop-shaped, placed anteroposteriorly, and more or less horizontal.

The transverse processes are short, stout, and unicipital with the distal ends irregular. They originate in front of the midpoint of the vertebra on the arch and centrum, and are strongly inclined posteriorly. Small anterior alar processes are present, but vertebrarterial foramina are lacking.

VARIATION ALONG THE COLUMN. *1. Cotyles.*- The centrum is deeply amphicoelous, with a small midcentral plug separating the two hollow cones of the cotyles. In end view, cotyles are subcircular, the anterior one being somewhat flattened on the ventral border; the posterior is produced ventroposteriorly. The posterior cotyle of the atlas has a ventral border is produced posteroventrally. The chordal foramen is dorsally located. The haemal arch covers the posterior two thirds of the centrum, surrounding a large haemal canal. The haemal crest is small, and the haemal process ends bicipitally in two robust, diverging points.

The neural canal is low, with an arched roof. A small spinal foramen is located just behind the dorsal arm of each transverse process. A low, thin neural crest occupies the posterior two thirds of the roof of the arch, running up the hyperapophysis. The latter is low and bicipital, ending in robust points, which extend behind the posterior zygapophyses. The posterior surface bears two small medial facets. Prezygapophyseal facets are oval, extended anterolaterally, and oriented more or less horizontally. They are situated well below the level of the roof of the neural arch. Postzygapophyseal facets are oval to teardrop-shaped, placed anteroposteriorly, and more or less horizontal.

The transverse processes are short, stout, and unicipital with the distal ends irregular. They originate in front of the midpoint of the vertebra on the arch and centrum, and are strongly inclined posteriorly. Small anterior alar processes are present, but vertebrarterial foramina are lacking.

VARIATION ALONG THE COLUMN. 1. *Cotyles.*- The centrum is deeply amphicoelous, with a small midcentral plug separating the two hollow cones of the cotyles. In end view, cotyles are subcircular, the anterior one being somewhat flattened on the ventral border; the posterior is produced ventroposteriorly. The posterior cotyle of the atlas has a ventral process that underlies the anterior cotyle of the following vertebra and bears two low basapophyses. The second cervical also has posterior basapophyses. In the trunk region further posterior, anterior basapophyses develop as long, low ventrolateral ridges. These basapophyses slightly underlap the posterior cotyle of the preceding vertebra.

The cotyles of the haemal vertebrae are circular. Throughout the column the cotyles are filled with significant amounts of calcified tissue, but remain relatively deeply concave. The anterior cotyle tends to have more infilling and, when adjacent vertebrae are separated in a skeleton, the notochordal tissue almost invariably stays with the anterior cotyle, perhaps indicating a proto-opisthocoelous condition.

2. *Hypapophyseal structures*.- A subcentral keel is absent throughout the column, making the centrum of hourglass shape in lateral view. The atlas and the first trunk vertebra often have posterior basapophyses. In larger specimens the vertebrae in the posterior two thirds of the trunk have low anterior basapophyses.

A haemapophysis is present on the caudal vertebrae, resembling an inverted neural arch. The haemal arch is long, enclosing much of the ventral surface of the centrum. The haemal crest is developed to the same degree as the neural spine of the same vertebra. At the posterior end, the haemal arch gives rise to two laterally divergent processes. Although these paired processes mirror the hyperapophysis, they are larger and more robust.

3. *Neural crest and hyperapophysis*.- The atlantal neural crest is robust and elongate. That of T1 begins at the anterior edge of the

neural arch and rises steadily to join the hyperapophysis. Throughout the anterior two thirds of the trunk, the neural crest is flat on top, extending horizontally from the hyperapophysis anteriorly. Midvertebrally, the crest then slopes down to the roof of the neural arch. In the posterior part of the trunk the crest is a thin ridge over the middle half of the vertebra. All but the most terminal caudals retain a neural crest as a small, triangular spike on the central part of the arch.

The hyperapophysis is robust, but not produced posteriorly. The neural arch rises above the anterior part of the posterior zygapophyses, terminating bluntly and bicipitally. On the rear surface is a pair of lateral facets, separated from each other by a median, vertical flange. The facets extend from the level of the postzygapophyses dorsomedially to the top of the hyperapophysis. In the trunk region the paired dorsal tips of the hyperapophysis each give rise to a small, ventrally directed flange of bone, which further divides the hyperapophyseal facets. In the posterior part of the trunk the hyperapophysis is lower and the facets face more ventrally. Postsacrally, the median flange disappears, leaving an undivided single facet on the posteroventral surface of each hyperapophysis. In the haemal series, the hyperapophysis ends in a forked process, the two rods diverging. Throughout the caudal series the hyperapophysis is bicipital, but this is less distinct posteriorly. In the most terminal caudals the hyperapophysis disappears.

4. *Zygapophyses*.- Prezygapophyseal facets of the trunk vertebrae are elongate and teardrop-shaped, extending anteroposteriorly with a very

slight anterolateral component. The facets become more oval in the haemal series and proceed more anterolaterally. Postzygapophyseal facets are inverted images of the prezygapophyses, being teardrop-shaped with the blunt end posterior. They extend posterolaterally with the lateral border tilted dorsally. Zygapophyses are present throughout the column until the last three or four caudal vertebrae.

5. *Transverse processes.*- Small lateral flanges are sometimes present on the atlas, but do not bear ribs. The transverse processes of T1 are robust, inclined posteriorly, and distinctly bicipital with the rib-bearers appressed. Dorsal and ventral arms are in a single vertical plane and a small vertebrarterial canal pierces each ventral arm. T2 is similar to T1: bicipital with closely appressed rib-bearers, no alar processes, dorsal and ventral arms in one vertical plane. However, the transverse processes are angled more posteriorly. T3 has smaller transverse processes and the rib-bearers are slightly divergent distally. The transverse processes extend posteriorly at about the same angle as that of T2, and the arms are in one vertical plane.

From T3 until the sacrum, the following trends occur: the dorsal and ventral arms become offset, the ventral ones being further anterior; the points of attachment of the transverse processes to the vertebra shift further posterior, until they originate midcentrally; the transverse processes become smaller and less strongly bicipital, the last two trunk vertebrae having unicipital transverse processes and sometimes lacking ribs. Alar processes are absent throughout the column, vertebrarterial canals are present in all trunk vertebrae, and subcentral foramina are lacking.

Postsacrally, transverse processes are reduced. In the first postsacral they are unicipital, attaching to the midpoint of the centrum and deflected slightly posteriorly. Small anterior alar processes are present and the vertebrarterial canals large. Although thin, the transverse processes are about the same length as those of the sacrum. In the caudal vertebrae, the processes extend laterally and somewhat posteriorly and decrease rapidly in size moving posteriorly.

Ambystoma talpoideum (Holbrook 1838)

Specimens.- One skeleton (UA 14335) and one cleared and stained specimen (UA 14424).

ATLAS. Anterior cotyles are widely separated and shallowly concave. In anterior view they are oval, with the axes extending dorsolaterally. In lateral view they are in the vertical plane. The odontoid process is a wide, long projection, grooved dorsally by the neural canal. There are no articulating facets on the odontoid process, but there is the remnant of a notochordal foramen. The general form of the odontoid is similar to that of *Scapherpeton*. The posterior cotyle is subcircular, but with the ventral half narrowing somewhat, and deeply concave. The chordal foramen is situated in the centre of the cotyle and a small amount of infilling is evident. A median subcentral keel may be present and there is a pair of posteriorly extending, spine-like posterior basapophyses.

The neural canal is wide and high, bounded by thin walls laterally. There is a wide, low neural crest, which is capped in cartilage.

A pair of rectangular surfaces rises dorsomedially from the postzygapophyses, comprising the hyperapophysis. A spinal nerve exits through the posterodorsal portion of each anterior cotyle.

No transverse processes are evident.

SECOND CERVICAL (T1). The second cervical is a short, high vertebra. The anterior cotyle is subcircular, but with the ventral half somewhat V-shaped. There is a small amount of calcification on the inner walls of the deeply concave cotyle, and the chordal foramen is centrally located. The posterior cotyle is as the anterior. but provided with small posterior basapophyses. There is no subcentral keel.

The neural canal is greatly enlarged, forming an approximately pentagonal shape in anterior view. A small projection of bone extends into the neural canal from the inner wall, opposite the origin of the dorsal arm of each rib-bearer. Small spinal nerve foramina pierce the walls of the arch anterior to the transverse processes. The neural crest is a simple, low ridge extending the length of the arch and formed by dorsomedial extension of the neural arch. The hyperapophysis is very broad and somewhat elongate. ending in a cartilaginous tip. A facet extends dorsomedially from the top of each posterior zygapophysis to the top of the hyperapophysis. Prezygapophyseal facets are teardrop-shaped and positioned anterolaterally with the lateral borders slightly raised. They do not extend far anteriorly and originate well below the top of the neural arch, which is not excavated between the anterior zygapophyses. The facets are slightly concave. Postzygapophyses have smaller, more elongate. teardrop-shaped facets.

These are oriented more or less anteroposteriorly, but with a minor posterolateral component. They are also slightly convex.

Transverse processes are robust and relatively short, with widely divergent rib-bearers. The ventral arms originate just in front of the midpoint of the centrum and extend straight laterally. Small anterior and posterior webs of bone (alars) join the proximal end of each arm to the centrum. The dorsal arms originate well back of the midpoint of the neural arch and extend slightly dorsally and posteriorly. The rib-bearers are joined by a web of bone along their proximal two thirds. The vertebrarterial canal may be quite large or very small.

TRUNK VERTEBRA (T8, see Fig. 7). Anterior and posterior cotyles are subcircular, slightly infilled, and have the chordal foramen placed centrally. This foramen is often incompletely plugged in smaller adults. There is no trace of a subcentral keel, but a pair of small, laterally elongate basapophyses is present.

The neural canal is large and, from the front, shows the form of a laterally elongate rectangle. The foramina for the spinal nerves are situated as in other *Ambystoma*. The neural crest is simply a small ridge. The hyperapophysis is robust, wide, and projects posteriorly. Its cap is tipped in cartilage. As in other *Ambystoma*, the posteroventral face of the hyperapophysis is provided with a pair of medially inclined depressions or facets. The hyperapophysis is similar to that of *Scapherpeton* in its elongation. Prezygapophyses rise anterolaterally and dorsally from the top of the neural arch. The facets are of irregular shape and large. Postzygapophyseal facets are smaller and in the form of elongate teardrops, extending posterolaterally. These are raised along their lateral borders and are somewhat convex.

The transverse processes are robust and short. Rib-bearers are widely separated and only slightly divergent. The ventral arms extend posterolaterally from the midpoint of the centrum and are buttressed to the latter by fenestrated ventral lamellae. The dorsal arms are only a half or a third of the diameter of the ventral, extending posterolaterally and somewhat dorsally from the posterior quarter of the neural arch. The rib-bearers are united by a web of bone proximally. Vertebrarterial canals are large.

SACRUM (T15). Excepting slight hypertrophy of the transverse processes and enlargement of the neural canal, the sacrum is very like the vertebrae immediately preceding it. Posterior and anterior cotyles are circular, the chordal foramen is central, and there are minor amounts of calcified infilling. The centrum is a thin spool of bone and deeply amphicoelous. There is no subcentral keel or basapophyses. A large subcentral foramen is present on one side or the other.

The neural canal is high and wide, as in much of the trunk. However, it is notably expanded and the neural arch is pierced by a pair of large foramina for the sacral nerves. The walls of the arch curve laterally about the expanded canal. The roof is gently arched and provided with a faint ridge, representing the neural crest. The hyperapophysis is robust and produced posterodorsally, but similar in proportions to that of the presacrals and postsacrals. It is tipped in cartilage and joined to the postzygapophyses by a web of bone on either side, which produces a pair of posteroventrally facing facets.

Prezygapophyseal facets are irregularly shaped ovals, with the long axis of each extending anterolaterally. They extend from the top of the roof of the neural arch, one on each side. The roof has a shallow, posteriorly directed notch between the prezygapophyses. Postzygapophyses have small, irregularly shaped facets, the lateral edges of which are upturned. The postzygapophyses are closely incorporated into the roof of the neural arch and the base of the hyperapophysis.

The transverse processes are not greatly enlarged. The ventral arms originate just forward of the midpoint of the centrum and extend posterolaterally in the horizontal plane. The dorsal arms originate behind the midpoint of the neural arch and proceed posterodorsolaterally. Rib-bearers are strongly bicipital and joined by a web of bone proximally. Very small alar struts unite the ventral arms to the centrum. There are small vertebrarterial canals.

HAEMAL VERTEBRA (H3). Both anterior and posterior cotyles are subcircular, with no infilling and a central chordal foramen. A thin notochordal plug of calcified tissue is present. The haemal arch arises along the length of the centrum, enclosing a large haemal canal. A large foramen pierces each of the walls. The haemal process is large and ends unicipitally, being subequal to the hyperapophysis.

The neural canal is large, the opening square in anterior view. A relatively large spinal nerve foramen is present in each wall of the arch. The neural crest is almost nonexistent, and the hyperapophysis is long, robust, and ends unicipitally. Prezygapophyseal facets are large and heart-shaped, with the apices facing posteriorly. Prezygapophyses extend out from the top of the neural arch and are raised dorsolaterally. Postzygapophyseal facets are small, irregular ellipses. They are applied on the ventrolateral sides of the hyperapophysis, with the axes extending posterolaterally. There is dorsolateral inclination.

Transverse processes are short, irregularly developed structures. They have a double origin: dorsally from the posteromedial portion of the walls of the neural arch and ventrally from the lateral walls of the anterior cotyle. Projections extend towards each other from each of these points of origin, often not meeting in the third haemal vertebra, but doing so in the first and second.

VARIATION ALONG THE COLUMN. 1. *Cotyles*.- Cotyles are subcircular and the centra deeply amphicoelous throughout the column, with small amounts of calcified infilling. Chordal foramina are centrally located and plugged by a thin wall of calcified tissue.

2. *Hypapophyseal structures*.- The subcentral keel is completely lacking, excepting a small one on the atlas in some individuals. The atlas, T1, and T2 have distinct, elongate posterior basapophyses. T3 lacks both anterior and posterior basapophyses in the sample available. The remainder of the trunk vertebrae have distinct anterior basapophyses, except for the immediately presacral vertebrae, which lack such structures. The sacrum and the two caudosacral vertebrae lack hypapophyseal structures. The remaining vertebrae have a fully developed haemapophysis, which comes to resemble closely an inverted neural arch, but lacking zygapophyses. The haemal spine ends bicipitally in much of the tail.

3. *Neural crest and hyperapophysis*.- The neural crest is nowhere strongly developed, being represented as a mere ridge on the roof of the neural arch throughout the postatlantal part of the column. The relatively robust, broad structures on the atlas may be designated the neural crest.

The hyperapophysis is a robust, relatively elongate spine, similar to that of *Scapherpeton*. That of the atlas differs from those of the rest of the column, being robust and nonprojecting. In large specimens, the hyperapophysis of T1 and T2 ends bicipitally, but in the smaller adult it is formed as in the remainder of the trunk. This may well indicate that the hyperapophysis is modified via paedomorphosis. Trunk vertebrae and the sacrum have a unicipital, robust spine that is tipped in cartilage and extends posterodorsally. The following vertebrae have a bicipitally ending hyperapophysis. In the most posterior caudals the hyperapophysis remains robust and posteriorly projecting. Small depressions are found on the posterolateral border of each hyperapophysis, extending dorsomedially from the top of each postzygapophysis.

4. *Zygapophyses*.- Prezygapophyses in T1 are irregularly shaped ovals. Posteriorly, the facets become progressively more elongate. The maximum anterolateral length occurs just behind the pectoral girdle. From here, moving back to the sacrum, the facets become less and less elongate. Throughout the trunk the long axes of the prezygapophyseal facets extend anterolaterally. All facets tilt up at the lateral edges and the anterior surfaces are somewhat curved ventrally. In the caudosacral area the facets are as on the sacrum (q.v.). Haemal

vertebrae have vaguely heart-shaped facets, as described above, with slight dorsolateral inclination. The roof of the neural arch is excavated posteriorly between the prezygapophyses, excepting in T1 and the more posterior haemals. Excepting T1, the prezygapophyses extend out from the dorsal surface of the neural arches.

Postzygapophyseal facets are smaller than those of the corresponding prezygapophyses. They are irregularly shaped to oval throughout the trunk, becoming highly irregular circles in the caudal vertebrae.

5. *Transverse processes.*- Transverse processes are lacking from the atlas. Those of the second cervical (T1) are short, robust projections extending almost straight laterally. Rib-bearers are bicipital and widely separated, but there is only slight divergence. Posteriorly, the rib-bearers come to extend progressively more posterolaterally. The zone of transition comprises T2 through T4 or T5. Rib-bearers become progressively reduced in diameter up to the sacrum. The dorsal arms are invariably the smaller and, from T4 on, shorter. There is posterodorsal tilt in lateral view, reflecting the orientation of the associated myomeres. A web of bone connects the proximal two thirds of the rib-bearers. Large vertebrarterial canals are developed throughout the trunk.

In the first postsacral vertebra the transverse processes are bicipital, but with the arms closely appressed and confluent. They extend laterally and slightly posteriorly and are relatively long. A small rib articulates to each transverse process in this vertebra, but posterior to this ribs are lacking. The first four or so postsacral vertebrae retain complete, unicipital transverse processes, which decrease progressively in length. From this point on, the transverse processes become highly irregular and are rapidly lost.

Alar processes are present as small, proximal shelves of bone buttressing the ventral arms to the lateral walls of the centrum. These are best developed anteriorly (maximum in T1), becoming progressively reduced posteriorly. Finally, immediately presacrally, they are represented by thin struts of bone on the posterior parts of the transverse processes. Relatively large subcentral foramina are present, on one side or the other, throughout the column.

Ambystoma tigrinum (Green 1838)

Specimens.- Eleven dry skeletons (UA 14336-14346) and seven cleared and stained specimens (UA 14426-14432). Descriptions are of young, postmetamorphic adults.

ATLAS (see Fig. 8). Anterior cotyles are small concave ovals, elongated horizontally. Facets are vertical in lateral view and situated below the neural canal. The odontoid process is long, wide, and flat, having a broad groove dorsally, over which the spinal cord passes. The posterior cotyle is round, but with the ventral border extended posteriorly and reinforced laterally by bony thickenings. There is no infilling and the chordal foramen is dorsal, in smaller specimens piercing the odontoid process. The ventral border extends under the anterior cotyle of T1. Hypapophyseal structures are limited to the posterior basapophyses and small, irregular subcentral foramina.

In anterior view the neural canal is oval, with the long axis vertical. Viewed posteriorly, it is in the shape of an inverted heart. The walls of the arch are robust, especially where they rise above the anterior cotyles. The roof is produced into a broad neural crest, which extends the length of the roof. The crest is finished in cartilage dorsally and the posterior part opens into a wide space, filled by the hyperapophyseal cartilage. A large foramen is located posterodorsal to the anterior cotyle on either side. Postzygapophyseal facets are small and teardrop-shaped, extended anteroposteriorly, and with the outer edges turned up.

Transverse processes are lacking.

SECOND CERVICAL (T1). The anterior cotyle is teardrop-shaped, the posterior subcircular. Both lack infilling and there are no projections from the cotylar rims. The centrum has a slight constriction, but remains notochordal well after metamorphosis in many specimens. A low, thick hypapophyseal ridge joins the cotyles and subcentral foramina are usually lacking, as are basapophyses.

The neural canal is high and large. A large foramen for the exit of the spinal nerve occurs posteriorly in each wall of the neural arch in some specimens. More often, these foramina are incompletely closed off posteriorly, or lacking. There are, however, two small foramina that pierce the walls of the arch anterior to the transverse processes, one just below each prezygapophysis. The neural crest is a low ridge running the length of the roof of the arch, which slopes down on either side of the crest. Posteriorly, the roof is raised into a low, wide hyperapophysis, which lacks posterior facets and is capped in cartilage. Prezygapophyseal facets are anterolaterally positioned ovals with the lateral edges raised. They project forward well in advance of the anterior cotyle. Postzygapophyseal facets are long and teardrop-shaped, with the posterolateral edges slightly upturned. They extend posterolaterally.

Transverse processes are short and robust, strongly bicipital with widely diverging arms. The ventral arms originate just anterior of the midpoint of the centrum and are angled posteriorly. The dorsal arms attach to the middle of the neural arch and are more strongly directed posteriorly. Therefore, the transverse processes are tilted from the vertical. Small, but distinct, ventral lamellae are present, and the vertebrarterial canals are large.

TRUNK VERTEBRA (T7, see Fig. 9). The anterior cotyle is subcircular, whereas the posterior is a laterally compressed oval. Both cotyles lack infilling and flanges on the rims. The vertebrae are notochordal in smaller postmetamorphic individuals, the centrum being a thin spool of bone covering the notochord with a constriction midcentrally. Hyperapophyses and basopophyses are lacking, although larger adults have small anterior basapophyses, which are developed as subcircular bumps. There are no subcentral foramina.

The neural canal is large and subcircular in end view. The roof of the neural arch is thick, sloping on either side from a median ridge. Small spinal nerve foramina are present, one piercing each wall just behind the transverse process. The hyperapophysis is a low, robust continuation of the roof of the arch, ending between the postzygapophyses and tipped in cartilage. There are two posteroventral facets, one dorsomedial to each posterior zygapophysis. Prezygapophyseal facets are elongate ovals, borne on long, narrow processes, which extend far anterolaterally. The anterior edges are somewhat raised. The prezygapophyses are buttressed to the anterior cotyle. Postzygapophyses project ventrally from the posterolateral borders of the hyperapophysis. The articular facets are diamond-shaped and extend posterolaterally with the internal edge dropped ventrally.

Transverse processes are distinctly bicipital, the ventral and dorsal arms diverging from each other and widely separated distally. The ventral arms originate just anterior of the midpoint of the centrum to extend laterally and somewhat posteriorly. The dorsal arms are about half the diameter of the ventral, originating at about the midpoint of the neural arch, and extending posterodorsolaterally. In some individuals, the transverse processes are almost at right angles to the vertebra, but in most they sweep somewhat posteriorly. These latter tend to be larger individuals. The rib-bearers are tilted in lateral view, the ventral arms being anterior to the dorsal. Both arms are of approximately the same length and very short, joined proximally by a web of bone. Alar processes are lacking and the ventral arms are pierced by wide vertebrarterial canals.

SACRUM. Both anterior and posterior cotyles are large circles, with no infilling, no flanges on the rims, and a large chordal foramen, which may or may not be plugged. There is no subcentral keel and basapophyses are lacking. Two large subcentral foramina are generally present, but some specimens have only one, on either the right or the left side.

The neural canal is high and wide, with a gently sloping, rounded roof. A large foramen for the spinal nerve is present in each wall of the neural arch behind the transverse process. There is no neural crest. The hyperapophysis is low, barely rising above the level of the postzygapophyses. It extends slightly posterior of the zygapophyses and ends in a pit, which is filled with cartilage in life. There are no hyperapophyseal facets. As in the trunk vertebrae, prezygapophyseal facets are elongate ovals, directed anterolaterally, with the outer edges raised slightly. Postzygapophyseal facets are diamond-shaped, extended posterolaterally, and more or less horizontal.

The transverse processes are enlarged and usually bicipital with the distal ends of the arms expanded. Both arms originate from the centre of the vertebra and are oriented, one above the other, in the vertical plane. The angle at which the transverse processes incline posteriorly varies from specimen to specimen. Some are almost at right angles to the sacrum, others are more strongly deflected backwards. However, the angles are of the same magnitude as seen in the preceding trunk vertebrae of the same specimen. The development of the bicipital condition is a function of age and size. In larval specimens (and neotenes) the transverse processes end unicipitally in a large oval. As metamorphosis and maturation proceeds, a constriction develops to cut the transverse process into two arms, which are, however, closely appressed. Anterior and posterior alar processes are variably developed, but always present. Large vertebrarterial canals are present.

HAEMAL VERTEBRA (H3). Anterior and posterior cotyles are vertically oval, lacking infilling, and with the rims not produced into flanges. The centrum is notochordal in postmetamorphic specimens. The haemal canal is large, with the haemal arch covering the posterior one half of the centrum. The haemal crest is a long, low ridge running the length of the arch. The haemal process is long and thick, extending posteroventrally and capped in cartilage.

The neural canal is low, with the roof gently arched above. A medium-sized spinal nerve foramen pierces each wall of the neural arch. There is no neural crest and the hyperapophysis is low and wide, extending just behind the postzygapophyses. It is somewhat bicipital and capped in cartilage. Prezygapophyseal facets are as in the trunk series, though smaller. Postzygapophyseal facets are diamond- to teardrop-shaped, and extend anteroposteriorly. They are smaller than those of the trunk series, being small protruberances from the lateral edges of the hyperapophysis.

Transverse processes are long, thin unicipital rods originating just anterior of the midpoint of the centrum. They extend more or less at right angles from the centrum, with a slight downward tilt. The transverse processes are buttressed to the centrum by anterior and posterior alar processes, and to the neural arch by vertical alars. There are relatively large vertebrarterial canals.

VARIATION ALONG THE COLUMN. 1. *Cotyles.*- The anterior cotyle in the trunk region is subcircular, but the posterior is more oval, owing to extension of the ventral rim of the cotyle. There is no infilling of calcified tissue and the vertebrae are notochordal, retaining a large continuous chordal foramen, which is closed off in larger specimens. The cotyles of the sacral and caudosacral vertebrae may be somewhat flattened dorsoventrally. Those of the caudal vertebrae are vertically oval.

2. *Hypapophyseal structures.*- A subcentral keel is present on the second cervical, but absent on all other vertebrae. Owing to the lack of a ventral lamella, subcentral foramina are generally lacking from the trunk vertebrae, but are present in the sacral and caudosacral vertebrae. The atlas has small posterior basapophyses and the second cervical shows traces of these structures. Anterior basapophyses are not developed in postmetamorphic individuals until they reach larger size.

The first caudosacral vertebra lacks hypapophyseal structures. On the second, however, a pair of low, thin hypapophyseal keels extends along the lateral edges of the centrum. The third postsacral carries a large, well-developed haemapophysis, being the first haemal vertebra. The haemal arch is a robust structure and remains present until the last three or so vertebrae in the tail. A low haemal crest may be present, the arch encloses a large haemal canal, and the walls are thin and pierced by a large foramen on one side or the other.

3. *Neural crest and hyperapophysis.*- In the atlas a robust neural crest extends the length of the arch, but is finished dorsally in cartilage. A crest is lacking throughout the trunk region, but the roof of the arch slopes steeply down from the median. A small neural crest is sometimes present on the haemal vertebrae.

The hyperapophysis is robust and present until the terminal caudal vertebrae. It is tipped in cartilage, leaving a large pit in skeletal specimens. In the trunk series the hyperapophysis ends on a level with the posterior edges of the postzygapophyses. Viewed posteriorly, each shows a pair of facets. These are triangular, the base running from the outer edge of the postzygapophysis medially to the midventral hyperapophyseal ridge. In the caudosacral vertebrae the hyperapophysis extends beyond the postzygapophyses. In the haemal series it is a long, hollow tube of large diameter extending posterodorsally.

4. *Zygapophyses*.- Zygapophyses are constant along the trunk, changing only in the caudal region. Prezygapophyseal facets are elongate ovals, extending laterally and somewhat anteriorly. The facets are inclined dorsolaterally, this tilting being especially marked in the first and second cervicals and gradually decreasing posteriorly. In the sacrum facets are nearly horizontal. Postzygapophyseal facets are approximately diamond-shaped, posterolaterally positioned, and inclined so as to conform to the corresponding prezygapophyses. In the caudal region zygapophyses are as in the trunk, but become smaller posteriorly. They are present until the final seven or eight vertebrae.

5. *Transverse processes*.- Atlantal transverse processes are absent. Those of T1 are distinctly bicipital with divergent arms joined by a web of bone. The ventral arms are slightly greater in diameter than the dorsal, originating on the centrum anterior to the point of attachment of the dorsal arms. The ventral arms are at right angles to the centrum, the dorsal are deflected posteriorly. Posterior alar processes are present and traces of anterior alars may be seen.

Posteriorly along the column, the transverse processes have the arms less widely divergent and smaller. Alar processes are usually not present, although very small anterior alars may remain. All postsacral vertebrae have unicipital transverse processes. In the caudosacrals the ventral lamellae are variably developed, but always present. The transverse processes extend laterally with a slight posteroventral component. In the haemals the transverse processes are progressively and rapidly reduced, disappearing at the sixth or seventh haemal vertebra.

v) Family Proteidae Hogg 1838

Necturus maculosus Rafinesque 1820

Specimens.- Six dry skeletons (UA 14347-14352) and one cleared and stained specimen (UA 14433).

ATLAS (see Fig. 10). The anterior cotyles are dorsoventrally flattened ovals on either side of the odontoid process and situated below the neural canal. In lateral view they are in the vertical plane and slightly concave. The odontoid process is a small, anteriorly directed spike, bearing part of the condylar facet on either side. The posterior cotyle is large and circular, with a small amount of uniform infilling. The rim is not extended and the chordal foramen is far dorsal. There are no hypapophyseal structures.

The neural canal is a large triangular opening in anterior view. Its base is the anterior cotyles, the sides are two thin struts rising from the centrum and merging dorsally to form the neural arch. There are small foramina in the neural arch, one dorsal to each of the anterior cotyles. Lateral flanges arise on the walls of the neural arch above the centrum. A low, broad neural crest runs the length of the roof of the arch. The hyperapophysis is not produced posteriorly, but has a pair of medial facets on the posterior surface for the attachment of muscles. The facets of the postzygapophyses are teardrop-shaped and extend anteroposteriorly. The zygapophyses arise from the posterolateral edges of the roof of the neural arch and extend posteriorly. The facets are strongly tipped from the horizontal.

SECOND CERVICAL (T1). The anterior cotyle is large and subcircular, with a small amount of uniform infilling. The chordal foramen is situated dorsally. The posterior cotyle is large, circular with no flanges on the rim, and with some calcified infilling. The chordal foramen is dorsal and the centrum is deeply amphicoelous. Two thick, parallel subcentral keels join the anterior and posterior cotyles. These have a horizontal ventral border. Subcentral foramina are absent, as are basapophyses.

The neural canal is relatively large and high, with a flat, narrow roof. There is a small internal flange on each wall of the neural arch just above the centrum. No spinal nerve foramina are present. A low neural crest occupies the middle three quarters of the roof. The hyperapophysis is low and extends posterior of the postzygapophyses. In one specimen the process ends bicipitally. Prezygapophyseal facets are irregular ovals, extending primarily anteroposteriorly, but with a slight anterolateral component. The lateral edges are strongly inclined, so as to correspond with the atlantal postzygapophyses. Postzygapophyseal facets are oval- to teardrop-shaped, positioned anteroposteriorly with the internal edges turned down.

The rib-bearers are long robust processes, bicipital but with the arms not diverging. An accessory flange extends dorsally along the length of each dorsal arm. The transverse processes originate just posterior of the midcentrum, at the posterior border of the neural arch and are swept posteriorly at a relatively steep angle. The ventral and dorsal arms are in the same vertical plane. Small first alar processes are present; the others are not developed. A small vertebrarterial canal pierces each transverse process dorsal to the alar process.

TRUNK VERTEBRA (see Fig. 12). Anterior and posterior cotyles are large and subcircular. They lack calcified infilling and the chordal foramen is situated dorsally. Flanges are lacking from the posterior cotyle. A small subcentral keel extends almost to the ends of the cotyles and two subcentral foramina are usually present. Basapophyses are lacking.

The neural canal is not depressed, but the roof is flat. Foramina for the spinal nerves are absent. The neural crest is a low, narrow ridge running the length of the neural arch to the hyperapophysis. The hyperapophysis is a low, long tube extending to, or beyond, the level of the postzygapophyses. There are no facets on the hyperapophysis. Prezygapophyseal facets are oval, extended anteroposteriorly and slightly anterolaterally, and with the lateral edges slightly inclined. Postzygapophyseal facets are teardrop-shaped, positioned anteroposteriorly, and with the lateral edges also inclined.

Transverse processes are relatively long and bicipital with slightly diverging arms. The transverse processes originate just posterior of the vertebral midpoint, extend posterolaterally, and are tilted from the vertical. The ventral arms are hollow tubes, the dorsal small, solid rods. The ventral lamellae are well-developed and small vertebrarterial canals are present.

SACRUM (T20). Excepting the large transverse processes, which bear the pelvic girdle, the sacral vertebra closely resembles the trunk vertebrae. Anterior and posterior cotyles are subcircular, lacking infilling, and have the chordal foramen located somewhat dorsally. Hypapophyses and basapophyses are lacking. A pair of subcentral foramina is generally found just behind the midcentral region.

The neural canal is high and broad. The roof of the arch is flattened and there are no foramina for spinal nerves. The neural crest is a low, narrow ridge, found over the hyperapophysis. The latter is a long, thin, hollow tube extending horizontally and posteriorly beyond the posterior zygapophyses. Prezygapophyseal facets are broad teardrops, extended anterolaterally with the outer edges slightly upturned. Postzygapophyseal facets are small, irregular diamonds, positioned anteroposteriorly. The facets are slightly inclined from the horizontal.

Transverse processes are long and robust, bicipital with slightly diverging arms, which are joined by a web of bone. The processes originate just behind the midpoint of the vertebra and are angled gently posteriorly. Dorsal and ventral arms are large, hollow cylinders, disposed in the vertical plane. There is a well-developed, but small, ventral lamella on each transverse process. Small vertebrarterial canals are present.

HAEMAL VERTEBRA (H3). Anterior and posterior cotyles are large and subcircular. There is no infilling and the chordal foramen is centrally located. The canal of the haemal arch is narrow and deep. Only the posterior third is arched. There is no haemal crest and the haemal process is a long, thin tube directed posteroventrally.

The neural canal is high and narrow with the roof of the arch curved above. There are no spinal nerve foramina, and the neural crest is lacking. The hyperapophysis is a long, thin tube directed posterodorsally and lacking facets. Prezygapophyseal facets are elongate ovals, positioned anteroposteriorly, and inclined from the horizontal. Postzygapophyses are often lacking from this haemal.

Transverse processes are variably developed on the third haemal vertebra. They may be absent, present on one side, or present on both sides. The transverse processes rapidly decrease in size through the haemal series, only being present on the first three or four. The processes are short and unicipital, originating midcentrally, and angled slightly posteriorly. Dorsal, ventral, anterior, and posterior alar processes buttress the transverse processes to the vertebra. Vertebrarterial canals are well-developed in the first two or so haemal vertebrae, but disappear subsequently.

VARIATION ALONG THE COLUMN. 1. *Cotyles*.- Cotyles are of constant development along the column, being circular to subcircular in outline. There is a small amount of infilling in the anterior part of the trunk, especially in larger specimens, but this does not make the cotyles shallower. The chordal foramen is dorsally located in each trunk vertebra, but is more central in the caudal series. Flanges are not present on any of the cotyles. The notochord is interrupted by a midcentral plug throughout the column.

2. *Hypapophyseal structures.*- There is no hypapophysis on the atlas, but T1 possesses a robust subcentral keel, divided medially by a longitudinal depression. A single heavy keel is present on T2. From this point posteriorly there is constant development of the hyperapophysis. In the trunk region it is dorsally concave in lateral view and does not extend to the ends of the cotyles. In the presacral vertebrae the extent of the hyperapophysis is reduced, and it is lacking from the sacrum. Posterior to the sacrum the hypapophysis is replaced by a haemal arch, which comes to be a ventral image of the neural arch.

Basapophyses are not present.

3. *Neural crest and hyperapophysis.*- The neural crest is best developed in the anterior part of the column. It often shows maximum extent on the atlas, with a progressive decrease posteriorly. A trace remains until the haemal series is reached. The crest extends the length of the roof in the atlas and T1. However, the anterior extent of the crest is reduced posteriorly. Through much of the trunk series a crest is present only on the posterior half of the roof and over the hyperapophysis.

The atlas lacks a hyperapophysis, but one is present on all subsequent vartebrae until the haemals are reached. In the atlas, the posterior part of the neural arch bears two facets, which face posteriorly and serve for the attachment of muscles. The hyperapophysis is present on the postatlantal vertebrae and facets are lacking. In some specimens the hyperapophysis of T1 ends bicipitally, but more often in this vertebra and the ones following the process is a unicipital tube. The hyperapophysis is dorsally inclined in the anterior part of the column. Posteriorly, it becomes lower and extended more directly posterior, especially in the last two trunk vertebrae and sacrum. The hyperapophysis extends slightly behind the postzygapophyses in most of the column, but becomes longer in the posterior region of the trunk and greatly extended in the caudal series.

4. *Transverse processes*.- A small flange extends posterolaterally from the posterodorsal part of each anterior cotyle of the atlas. T1 has a well-developed, distinctly bicipital transverse process on each side. Except for a trace of the posterior alar processes, ventral lamellae are not developed. In the second trunk vertebra the anterior alar processes are represented by small ridges on the ventral arms of the transverse processes. The dorsal arms are hollow tubes with thick accessory flanges along their dorsal edges. Posteriorly, the dorsal arms are suppressed, although they reappear on the sacrum. The ventral arms remain tubular, and a vertical flange rises from each to join an accessory flange from the roof of the neural arch.

Transverse processes are tipped from the vertical, such that the dorsal edges are further posterior than the ventral. In the posterior part of the trunk the rib-bearers are more closely appressed. The ventral lamellae are well-developed throughout the column, except for the haemal series, reaching a maximum extent in the caudosacrals and posterior presacrals.

In the caudosacrals the dorsal flanges and arms are lacking from the transverse processes, leaving the ventral arms and dorsal ridges of bone. The ventral lamellae are present until the third or fourth haemal vertebra. On or about the fourth haemal the transverse processes disappear.

5. *Zygapophyses*.- Prezygapophyses are anterolaterally disposed throughout the column and the lateral edges are deflected dorsally. The facets are oval to teardrop-shaped. Postzygapophyseal facets are oval or irregular and extend posterolaterally. The articulating surfaces are largely horizontal, excepting those of the atlas, but with a slight dorsal deflection of the lateral edge.

In the trunk the zygapophyses are relatively widely separated, imparting an hourglass shape to the vertebra in dorsal view. This separation is reduced in the last trunk vertebra and in the sacral, with the trend continuing posteriorly. Zygapophyses are rapidly reduced in size in the haemal series, disappearing in the fourth or fifth haemal vertebra.

vi) Family Plethodontidae Gray 1850

Plethodon jordani Blatchley 1901

Specimens.- Three dry skeletons (UA 14353-14355) and one cleared and stained specimen (UA 14434).

ATLAS. The atlas is finely formed and delicate. Anterior cotyles resemble dorsoventrally elongate beans, convex laterally, and flattened medially. They extend somewhat below the neural canal. There is posterodorsal inclination in lateral view and the articular surfaces are flattened. The odontoid process is a long, wide projection formed of thin bone. A tall, thin plate rises from the base of each anterior cotyle to half of the latter's height. These face laterally and somewhat ventrally, so as to form facets for articulation with the occipital condyles of the skull. The odontoid forms a ventral cup-like structure over which the spinal cord passes. The posterior cotyle is subcircular and deeply concave, with a moderate amount of infilling anteriorly. The ventral border extends posteriorly and, in larger specimens, traces of posterior basapophyses are present. No other hypapophyseal structures are evident. Subcentral foramina are present, but small and irregularly spaced.

The neural canal is large and higher than wide. The neural arch is thin and gently convex laterally. Two relatively large foramina, one behind each anterior cotyle, provide exits for spinal nerves. The roof of the arch is gently swollen and projects anteriorly above the odontoid process. A wide, low neural crest, which is finished dorsally in cartilage, runs most of the length of the roof. The hyperapophysis is low and excavated between the posterior zygapophyses. A pair of low, medially merging ridges extends anteriorly from the top of each postzygapophysis. These form a low aliform process. Postzygapophyseal facets are small, elongate teardrops, which are raised posteriorly and laterally.

Transverse processes are lacking.

SECOND CERVICAL (T1). The anterior cotyle is small and teardrop-shaped, with a moderate amount of infilling. The posterior cotyle is larger and slightly compressed dorsoventrally. The centrum is deeply amphicoelous. Subcentral foramina are lacking and, excepting small posterior basapophyses, hypapophyseal structures are absent.

The neural canal is large, the walls of the arch being expanded laterally beyond the centrum. The roof of the arch is expanded, with a well-developed neural crest running along the midportion, but not reaching to the anterior of the arch or to the hyperapophysis. The latter is a gently raised structure similar to that of *Triturus cristatus*. It forms a raised dome between the postzygapophyses. The neural arch is pierced by small foramina in front of the rib-bearers. Prezygapophyseal facets are greatly elongate, narrow structures projecting for half their length beyond the neural arch. The facets are pointed anteriorly and posteriorly and are gently, but distinctly, raised laterally. Postzygapophyseal facets are also elongated, but with the posterior part wider than the anterior. This produces an irregular teardrop, but with the rear edge being more angular (i.e., diamond-shaped). The postzygapophyses project behind the hyperapophysis.

Transverse processes are small with delicate but widely separated rib-bearers, which are connected by bone for their proximal one half. Dorsal and ventral arms are of subequal diameter, extending posterolaterally at the same angle, but with the ventral arms anterior to the dorsal. The dorsal rib-bearers are longer than the ventral. Large ventral lamellae are developed at the base of the ventral rib-bearers, producing a flat surface on the underside of the vertebra. The ventral lamellae are closely associated with the expanded walls of the neural arch.

TRUNK VERTEBRA (T8, see Fig. 14). The centrum is deeply amphicoelous. The anterior cotyle is subcircular, but with the dorsal rim flattened, and there is a small amount of irregular infilling. The posterior cotyle is larger and distinctly wider than high. There is slight infilling. Subcentral foramina are lacking and there is no subcentral keel, the base of the centrum being concave dorsally. Posterior basapophyses are usually developed. They are elongate and situated on the lateral edges of the posterior cotyle.

The neural canal is large and significantly wider than high. The walls of the arch extend laterally beyond the edges of the centrum. The roof of the arch is gently swollen, with a low, peaked neural crest located in the second one quarter of the roof from the front. The hyperapophysis is low and ends in a pair of short, blunt posterior projections. These do not extend beyond the posterior zygapophyses and are fully finished bone. Foramina for spinal nerves pierce the neural arch, one on either side just posterior to the transverse processes. Prezygapophyses are elongate, narrow facets that do not extend far beyond the roof of the neural arch. They are widest anteriorly and gently inclined laterally. Postzygapophyses are more symmetrical, elongate teardrops, with the narrow point extending anteriorly. The articular surface is gently concave dorsally.

The transverse processes are small and short, bicipital structures extending laterally and posteriorly. The ventral arms are of greater diameter than the dorsal, which extend upwards as well as posterolaterally. There is little webbing, the rib-bearers being free for almost the entire length. There are no ventral lamellae. A small vertebrarterial canal pierces each ventral rib-bearer and is underlain only by a thin strut of bone.

SACRUM. The sacrum is in the region of T18, but may occur on T17 or T19. Its anterior cotyle is subcircular, but irregularity in shape is common. The larger posterior cotyle is somewhat wider than high. The centrum is deeply amphicoelous with irregular infilling by calcified tissue near the chordal foramen. Subcentral foramina are usually lacking, but, if present, they are irregular. There is no subcentral keel and basapophyses are absent.

The neural canal is large and slightly wider than high. The walls of the neural arch bulge laterally beyond the centrum. The roof of the arch is flat and supports a low, indistinct crest. The crest is longer, but not significantly higher, in larger individuals. The low, short bicipital hyperapophysis rises gently posteriorly from between the postzygapophyses. Spinal nerve foramina are large holes, one on either side, located just posterior to the origin of the transverse processes and facing posterolaterally. Prezygapophyseal facets are wider than those of the midtrunk region. They are teardrop-shaped and directed anteriorly and slightly laterally. Their anterior extent is only about one third of their total length past the front of the neural arch, which is not excavated posteriorly between the zygapophyses. There is slight dorsolateral inclination. The postzygapophyses are proportionally even broader than are the anterior. They are irregularly shaped teardrops, slightly upturned laterally and dorsally concave.

Transverse processes are robust with rib-bearers of large diameter. They extend laterally and somewhat posteriorly, with the dorsal arms situated behind the ventral. The ventral arms are in the horizontal plane, whereas the dorsal ones extend dorsolaterally. The ventral arms are dorsoventrally flattened distally, but the dorsal ones are more circular. Strictly speaking, ventral lamellae are not present. However, owing to the lateral spread of the neural arch and the buttressing of the ventral rib-bearers to the rest of the vertebra, the ventral surface on either side of the centrum is wide and flattened.

HAEMAL VERTEBRA (H3). Both anterior and posterior cotyles are deeply concave with a moderated amount of dense calcified infilling. The anterior cotyle is wider than high, with the dorsal border produced anteriorly. The posterior cotyle is subcircular, its ventral border slightly posterior of the dorsal. The haemal arch runs the length of the centrum. Its canal is small, appearing circular in anterior view. There are two low lateral crests on the arch and a well-developed haemal crest, which is, however, not produced ventrally. Posteriorly the haemal arch extends ventrally, producing a haemal process. A large foramen often pierces one side or the other of the haemal arch.

The neural canal is depressed, but relatively large. The neural arch is gently expanded above, with a distinctly raised crest occupying the second anterior one quarter. The rear of the arch is low, the hyperapophysis consisting of a pair of widely divergent, indistinct dorsal ridges. The spinal nerve foramina are small and located at the dorsal edge of the wall of the neural arch, immediately behind each transverse process. Prezygapophyses are relatively large, extending well lateral and anterior to the arch. Facets are wide anteriorly and then gently tapering for the posterior third. There is slight dorsolateral inclination. Postzygapophyses are relatively smaller and less elongate than the prezygapophyses, although still of greater distance anteroposteriorly than lateromedially.

Transverse processes are unicipital, elongate, thin, and posterolaterally directed.

VARIATION ALONG THE COLUMN. *1. Cotyles*.- The anterior cotyle of T1 is slightly teardrop-shaped. That of the next six or seven vertebrae is subcircular. Throughout the remainder of the trunk, up to and including the sacrum, the anterior cotyle is slightly wider than high. This is especially marked in larger specimens. The anterior cotyle of the first caudosacral is circular, that of the second is laterally elongate, as is that of the first few haemals. In the haemal series the dorsal rim of the anterior cotyle is set further forward than the ventral.

The posterior cotyle is of greater diameter than is the anterior one of the same vertebra (? pro-opisthocoely), but it otherwise more or less mirrors the form of the articulating anterior cotyle. Infilling is minimal in the trunk region, being perhaps more pronounced in the anterior cotyles. The caudosacrals and first few haemals have significantly more infilling of both cotyles.

2. Hypapophyseal structures.- A subcentral keel is completely lacking. Faint, relatively elongate lateral ridges are present on the posterior part of the centrum in the trunk vertebrae. However, these posterior basapophyses are not seen in some specimens, especially, but not necessarily, in smaller individuals. The third postsacral vertebra bears the first haemal arch. This arch fails to extend anteriorly for the entire length of the centrum and lacks haemal and lateral crests. The second haemal vertebra is transitional between this and the fully developed condition (see above). The haemal arch is of constant development along the caudal series. The haemal crest is larger than the neural crest of any given vertebra.

3. *Neural crest and hyperapophysis*.- The neural crest is present on the atlas as a low, long boss. In vertebrae of the pectoral region (T1 and T2) the crest is relatively long and high. From here posteriorly, the crest becomes progressively shorter and lower. In the post-pectoral region the crests are peaked dorsally. In the six or seven vertebrae anterior to the sacrum the neural crest is a low ridge on the anterior part of the arch. From the caudosacral vertebrae posteriorly there is a gradual increase in relative height and length of the crest.

The hyperapophysis is a relatively low structure terminating in two posterior projections. In the forward part of the trunk it is weakly bicipital. The haemal vertebrae, however, have a distinctly and widely bicipital, although short and low, hyperapophysis.

4. *Zygapophyses*.- Prezygapophyses of the pectoral area (T1 to T3) are elongate, tapering anteriorly and posteriorly, and raised laterally to a significant degree. The facets extend well forward of the neural arch, which is, however, not excavated between them. They are aligned anteroposteriorly. Behind the pectoral area, the facets become progressively broader, but retain a primarily anteroposterior position. Presacrals, sacrals, and caudosacrals have less elongate facets. There is a distinct anterolateral extension and the lateral edges are markedly inclined dorsally. In the haemal vertebrae the prezygapophyses are proportionally enlarged, flaring laterally and anteriorly from the neural arch.

Postzygapophyses are smaller than the corresponding prezygapophyses, and tend to be shorter and broader.

5. *Transverse processes*.- There is no trace of transverse processes on the atlas. Their development throughout the trunk region is relatively

constant. They are distinctly bicipital with well-separated rib-bearers. The latter are short and very thin, extending posterolaterally from the neural arch. The dorsal arms are set posterior of the ventral, causing each transverse process to be tilted. The transverse processes are constantly developed along the trunk, until the first two or so presacrals, which have reduced transverse processes. The first presacral often lacks dorsal rib-bearers and ribs are absent.

The transverse processes of the postsacral region are elongate, unicipital, and directed posterolaterally. There is no discontinuity in the form of the transverse processes between the caudosacrals and haemals; they simply become gradually shorter and finally all but disappear.

Desmognathus fuscus (Rafinesque 1820)

Specimens.- Three dry skeletons (UA 14360-14362) and two cleared and stained specimens (UA 14449, 14450).

ATLAS (see Fig. 15). In anterior view the atlas appears as three circles: the central, dorsal circle is the neural canal and, to each side and slightly ventral, are the paired anterior cotyles. The latter are deep fossae for articulation with the occipital condyles of the skull. An odontoid process is lacking, except as a thin flange extending between the cotyles. Just dorsal to this, on the medial side of each cotyle, is a pair of small, anteriorly directed, bony spikes. The centrum is only developed in the posterior half of the atlas. It is angled ventrally below the level of the anterior cotyles, giving the appearance of being an appendage of the latter. The posterior cotyle is circular and filled anteriorly with calcified cartilage, which leaves a small rim to surround the condyle of the second cervical. There are two well-developed posterior basapophyses.

The roof of the neural arch extends straight back from the top of the anterior cotyles and then rises smoothly to its posterior border. The roof is flat and the neural crest is weakly developed or lacking. The walls of the arch are formed by the dorsally extending anterior cotyles. Inside the arch two small flanges are present just above the centrum. A small foramen pierces each anterior cotyle posteriorly. The neural arch is robust, wide, and very high in the hyperapophyseal region, where there is a posteriorly facing pair of facets. Above the postzygapophyses are laterally expanded flanges, which run dorsally along the side of the neural arch. In posterior view the hyperapophysis forms an extensive area for the insertion of muscles, with the lateral flanges above the postzygapophyses further increasing the area. The posterior zygapophyses are small, roughly triangular in shape and strongly raised laterally. The facets are weakly convex.

There are no transverse processes.

SECOND CERVICAL (T1). T1 is robust, notably more sturdy and broader than the following trunk vertebra. There is a hemispherical, robust anterior condyle that fits into the atlantal cotyle. The large posterior cotyle is a laterally elongate oval, with infilling anteriorly to form a shallow cup. The ventral rim is not posteriorly extended and the dorsal rim is slightly excavated anteriorly. A robust projection extends ventrally and somewhat anteriorly from behind the condyle. This fits between the posteriorly projecting basapophyses of the atlas. Large, laterally and posteriorly expanded, posterior basapophyses are present. There are two small subcentral foramina and, excepting the single anterior flange, there is no subcentral keel, the centrum being excavated dorsally.

The neural canal is large and approximately diamond-shaped in anterior view, with the roof sloping relatively steeply above. The roof projects anteriorly between the prezygapophyses. A small foramen pierces each wall of the neural arch, just posterior to the prezygapophyses. The arch is expanded laterally past the centrum. A well-developed, high neural crest extends almost the entire length of the roof of the arch. The rear of the arch rises steeply between the postzygapophyses, to produce a high, wide hyperapophysis with a posteriorly facing area for the insertion of trunk musculature. A large, long pterygapophysis (see Wake 1966) extends posterolatero-dorsally from the surface of each postzygapophysis. Prezygapophyses are not greatly offset from the neural arch, but extend anterolaterally a short distance beyond the arch. The facets are of irregular teardrop shape and broad anteriorly. They are notably anteroventrally tipped and slightly raised laterally. Prezygapophyses are widely separated and originate below the roof of the arch. Postzygapophyses are vaguely teardrop-shaped, situated nearly horizontally, and widely separated.

Transverse processes are elongate, robust structures originating solely from the walls of the neural arch. They are distinctly bicipital with the arms joined by a bony web. Dorsal and ventral arms are in a single vertical plane, with the ventral arms extending posterolaterally and, for their distal half, slightly dorsally. Dorsal arms proceed posterodorsolaterally and are of greater diameter than the ventral. A large, ventrally flattened, ventral lamella is present on either side of the centrum and a large, circular vertebrarterial canal pierces each ventral rib-bearer.

TRUNK VERTEBRA (T8, see Fig. 16). A well-developed anterior condyle is present, formed of calcified cartilage. It is in the form of a ball, but with a vertical depression anteriorly and a small chordal foramen. The posterior cotyle is shallow, dorsoventrally compressed, and with the body of the centrum filled with calcified cartilage so as to produce a flat anterior and internal surface. The tissue is pierced by a very small chordal foramen. Plate-like posterior basapophyses extend posterior to the cotyle. A single, medial hypapophysis is situated just behind the condyle. The centrum is deeply concave dorsally in the midportion and lacks other projections ventrally.

The neural canal is large, bean-shaped in anterior view, and with the roof of the arch gently rounded above. The walls of the arch extend lateral to the centrum and are pierced by a spinal nerve foramen, facing posterolaterally, immediately behind each dorsal rib-bearer. A small, low neural crest occupies the roof of the arch at the level of the attachments of the transverse processes. The hyperapophysis is a direct continuation of the roof of the arch, extending posterodorsally to end bicipitally in two distinct processes, which extend behind the postzygapophyses. Small, but distinct, pterygapophyses are present. Prezygapophyseal facets are oval, but with flattened medial borders. They extend anterolaterally from below the top of the roof of the arch, to barely in front of the anterior condyle. They are relatively widely separated. Postzygapophyses are elongate teardrops, slightly raised laterally, and with the articular surfaces somewhat concave.

The transverse processes are distinctly bicipital, the dorsal and ventral arms originating on the neural arch just posterior to the postzygapophyses. The dorsal arms are somewhat behind the ventral, extending posterodorsolaterally, while the ventral proceed posteroventrolaterally. The arms are joined by bone proximally and are well-separated distally. The ventral arms bear anterior projections on the distal thirds, these being reduced from the condition further forward along the column. Proximally the ventral arms expand into heavy ventral lamellae, which are pierced by subcentral foramina. There is a large vertebrarterial canal through each transverse process.

SACRUM (T16). The condyle is robust, with a deep, wide vertical groove anteriorly. It is circular except for a flattened dorsal edge. A small chordal foramen is retained. The posterior cotyle is a laterally elongate oval with a flattened dorsal rim. It is significantly deeper than those of the anterior trunk vertebrae, but is still provided with anterior infilling. There is no hypapophyseal keel and no posterior basapophyses, but laterally displaced subcentral foramina are present.

The neural arch is large and wide, appearing bean-shaped in anterior view. The roof is gently domed and the walls of the arch are laterally expanded. Spinal nerve foramina are large, each extending posterolaterally through a channel in the transverse process. A low neural crest is situated anteriorly and the hyperapophysis rises gently posterodorsally and ends bicipitally in two widely separated projections. There is no trace of pterygapophyses. Prezygapophyseal facets are large irregular ovals, which are strongly raised laterally. They extend anterolaterally and are well lateral and somewhat anterior to the neural arch. Postzygapophyses are much smaller, irregular ovals or teardrops with pronounced dorsolateral inclination. They are shallowly concave dorsally.

Transverse processes are expanded, the arms greatly enlarged distally, slightly divergent, and joined by bone along their lengths. They arise from the neural arch, the dorsal arms well posterior of the ventral, thus producing deflected transverse processes. Ventral arms extend posterolaterally, the dorsal posterodorsolaterally. A large ventral lamella is present on each ventral rib-bearer and there is a small vertebrarterial canal. The centrum is small midvertebrally, the centre being dish-shaped in ventral view, owing to this and to the conformation of the ventral lamellae.

HAEMAL VERTEBRA (H3). The opisthocoelous condition is well-developed, as in the trunk vertebrae. The condyle resembles that of a newt, being of greater anterior extent dorsally than ventrally. The posterior cotyle is a laterally elongate oval. The haemal arch is well-developed, extending the length of the centrum posterior to the condyle. The arch is low, but sends out a long, bicipital haemal process. This is distinctly larger and much longer than the hyperapophysis of the same vertebra, extending posteriorly and, especially, ventrally. A long, deep, and thin haemal crest is present, expanded ventrally in the anterior part. This also recalls the condition in newts.

The neural crest is minute and the hyperapophysis rises posterodorsally a slight distance and ends bicipitally. Anterior and posterior zygapophyses are well-developed, elongate, and strongly raised laterally.

The transverse processes are essentially vertical flanges of bone, angled posteriorly, and with distinct ventral lamellae.

VARIATION ALONG THE COLUMN. 1. *Condyles and cotyles*.- The condyle is a robust ball throughout the column, with a vertical, anterior groove in each of the anterior trunk vertebrae. In the more posterior trunk vertebrae the condyle is flattened anteriorly, while in the caudal vertebrae it is flat anteriorly, but with the dorsal part further forward than the ventral. This recalls the situation of the salamandrid newts.

The atlantal posterior cotyle is circular, but more posteriorly the cotyle is oval in the lateral plane, with a tendency to develop a flattened dorsal rim. The oval becomes more pronounced in the posterior trunk region and caudal regions. Each cotyle is more oval than the articulating condyles perhaps allowing more freedom of movement of the ball-and-socket joints (see below).

A chordal foramen is present in the posterior cotyle and anterior condyle. The cotyle is infilled so as to produce a shallow cup. There is no infilling along the inner walls where the condyle inserts.

2. *Hypapophyseal structures*.- The hypapophysis is represented by a ventrally and anteriorly directed spine beneath the anterior cotyle. This is present starting with T1, increases to maximum at the fourth trunk vertebra or so, and from here decreases gradually. In *D. monticola* (snout-vent length 42 mm, UA 14447) these hypapophyses disappear in the midtrunk region. In smaller specimens of *D. fuscus*

(snout-vent length 44 mm, UA 14449) they also disappear in the midtrunk area. However, in larger specimens only the first presacral lacks all trace of the anterior hypapophyseal projection. In very large *D. fuscus* in the forward trunk region the ventral part of the hypapophyseal spine is expanded into a boss.

The hypapophysis is closely associated with the posterior basapophyses of the next anterior vertebra. The size of the hypapophysis is correlated with that of the baspophyses, large basapophyses projecting beside a large hypapophysis. The more anterior, larger basapophyses end bicipitally in two small projections, one above the other. Although hypapophyses may disappear along the trunk, basapophyses remain present, even if only as small ridges. The first presacral, sacral, and caudosacrals lack basapophyses.

A haemal arch is developed on the caudal vertebrae. The haemal process ends bicipitally and extends posteriorly and, especially, ventrally. The arch is low, robust, and bears a well-developed haemal crest. This crest is high, forming an anteroventrally projecting triangle on the haemal process and arch. The haemal process and crest are present and well-developed on the most posterior caudal vertebrae.

3. *Neural crest and hyperapophysis*.- The neural crest is variably developed through most of the column. In the trunk series, maximum development is on the second cervical, with decrease posteriorly. Smaller specimens have the crest only on the second cervical; however, in larger individuals a crest is present, but low and thin, on all trunk vertebrae. In *D. monticola* the crest in the trunk region is variably present, being a small, medial bump when developed. In this species the second cervical lacks a crest.

In the caudal series, the neural crest is somewhat higher, but dwarfed by the haemal crest. Smaller specimens lack a neural crest on the caudal vertebrae.

The hyperapophysis is usually vertical with posteriorly facing surfaces in the atlas and T1. That of the trunk vertebrae is low and extends to the posterior edge of the postzygapophyses. It ends bicipitally with widely separated tips. By contrast, the hyperapophysis of *D. monticola* is tricipital, with a small median projection between the two lateral processes in the trunk region. Caudal vertebrae have bicipital hyperapophyses in both species.

4. *Zygapophyses*.- Prezygapophyses are well set off laterally from the neural arch. They are relatively strongly raised laterally, this being minimum in the posterior trunk region and maximum in the caudal vertebrae. Facets are elongate ovals, extending anteroposteriorly and with a tendency to have the anterior and posterior ends pointed. Postzygapophyses are smaller than the corresponding prezygapophyses and in the form of teardrops, with dorsolateral inclination. The anterior trunk vertebrae, but not the atlas, have well-developed, posterodorsolaterally extending pterygapophyses. These are large on T1 and decrease progressively from here on, to disappear in the area of T10.

5. *Transverse processes*.- There are no atlantal transverse processes. On T1 the processes are distinctly bicipital, the arms joined by a web of bone. They have slight posterior inclination, dorsal and ventral arms being in a single vertical plane and both angled dorsally. Posterior alars are present. Further back, the transverse processes remain bicipital and extend at right angles to the vertebrae, coming

off the side of the neural arch with no attachment to the centrum. Dorsal and ventral arms tend to remain in one vertical plane until the posterior region of the trunk, where they are tilted in line with the myosepta.

The first presacral does not bear ribs. The ventral arms of the transverse processes are robust, whereas the dorsals are represented by posteriorly deflected flanges. Those of the sacrum are angled posteriorly to a greater degree than those of the trunk vertebrae. In most salamanders the transverse processes of the sacrum are vertical, but in this species they are tilted posterodorsally. The caudosacral vertebrae have unicipital transverse processes with well-developed anterior and posterior alar processes. There is a dorsal vertical flange on each process and the process is deflected posteriorly and ventrally. In the caudal vertebrae, the transverse processes are progressively reduced and change orientation to become vertical flanges. Transverse processes are present far caudally.

Alar processes are relatively well-developed along the column, especially in larger individuals. Owing to the small midpart of the centrum and the large alars, the vertebrae are dorsally concave. In the anterior trunk vertebrae are found anterior extensions of the ventral rib-bearers, correlating with the subvertebral myomeres (q.v.).

vii) Family Salamandridae Gray 1825

Salamandra Laurenti 1768

Specimens.- One skeleton (UA 14366) of *Salamandra atra*, one skeleton (UA 14365) and two cleared and stained specimens (UA 14451, 14452) of

Salamandra salamandra. The two available species are similar. Where pertinent, differences have been noted.

ATLAS (see Fig. 17). Anterior cotyles are oval and the long axes are dorsoventral, such that the ventral borders are closer together than are the dorsal. Articular facets are shallow basins. Between the ventral borders of the two cotyles a thin, elongate odontoid process juts anteriorly. From its lateral edges two flanges rise dorsolaterally. These have lateral facets for articulation with the medial surfaces of the occipital condyles. The posterior cotyle is oval in the horizontal plane, deep but plugged anteriorly with calcified tissue. There are no basapophyses and a hypapophysis is lacking.

The neural canal is large and diamond-shaped in anterior view. The base of the diamond is the odontoid process, the medial borders of the anterior cotyles form the two lower edges, and the walls of the neural arch rise and converge medially to form the top sides. The roof of the arch is steep and continues into a well-developed neural crest. This crest may be thin (*S. atra*) or very thick and finished dorsally in cartilage (*S. salamandra*). The anterior edge of the roof flares forward into two thin flanges, one on either side of the midline. On each side of the anterior part of the neural crest a small flange drops ventrally. The hyperapophysis rises vertically between the postzygapophyses. Posteriorly, a facet originates above each zygapophysis and extends dorsally and slightly medially to meet the posterior edge of the neural crest. Postzygapophyses have teardrop-shaped facets, the blunt part posterior. They are horizontal and slightly concave.

SECOND CERVICAL (T1). The anterior condyle is a dorsoventrally compressed oval with the dorsal portion anterior of the ventral and a large depression anterior. Thus it does not form a true ball-and-socket joint with the atlas, but interlocks with the atlantal posterior cotyle. The posterior cotyle is also oval with a flattened dorsal rim. There is no infilling except far anterior and the cup is very deep. There are no basapophyses or subcentral keel. Subcentral foramina are large and irregular.

The neural canal is large and in the form of a pentagram, the base formed of the centrum with the walls of the neural arch producing the other sides. The walls of the arch are pierced by several foramina: two small ones, one on either side just posterior to each prezygapophysis, and larger ones posteriorly behind the transverse processes. The latter may be divided into two parts by a bridge of bone. A relatively high, thin neural crest extends the length of the roof of the arch. The hyperapophysis is relatively low, produced by a rising of the neural arch between the posterior zygapophyses. A pair of smoothly curved flanges forms the posterior border, to which attach the hyperapophyseal septa. Prezygapophyses are broad ovals, extending anteroposteriorly and slightly laterally. They are widely separated and originate below the top of the roof of the arch. Postzygapophyseal facets are large, broad teardrops. Both anterior and posterior facets are raised laterally and both zygapophyses are joined to the dorsal rib-bearers by a lateral flange of bone, which increases the area of the roof of the arch.

Transverse processes are robust but not enlarged. They are slightly inclined from the vertical and the arms are not divergent, but relatively widely separated — the ventral originating from the centrum and the dorsal from the top of the wall of the arch. They are joined by bone along their lengths. Large ventral lamellae are present on the ventral rib-bearers, especially formed by the posterior alar processes. A large, twisted vertebrarterial canal pierces each ventral arm.

TRUNK VERTEBRA (T8, see Fig. 18). A plug of calcified cartilage extends forward from the anterior cotyle. However, it is shallowly concave anteriorly. The posterior cotyle is a flattened oval, the lateral and ventral sides extending further posterior than does the dorsal. There is no infilling of the cotyle and no closure of the notochordal canal until it is blocked by the calcified tissue of the anterior cotyle. Hypapophyseal structures are lacking.

The neural canal is large and the neural arch is not depressed. A well-developed, but low, neural crest is present midvertebrally. The arch rises gently posteriorly, accommodating two lateral facets, which face posteriorly. A spinal nerve foramen pierces the arch just posterior to each dorsal arm of the transverse processes. Prezygapophyseal facets are large, broad ovals extending anterolaterally. They are widely separated, originate from the top of the roof of the arch, and are raised laterally. Postzygapophyseal facets are also large, but approximately teardrop-shaped and gently concave dorsally. The roof of the arch is widened by zygapophyseal flanges joining to the transverse processes from the anterior and posterior zygapophyses.

The transverse processes are distinctly bicipital, the arms close together and united by thin webs of bone. The ventral arms arise on the centrum anterior to the medial constriction. The dorsal arms originate on the sides of the neural arch posterior to the origins of the ventral arms. Both are angled posteriorly, but to different degrees, such that distally they are in a single vertical plane. The ventral arms are each pierced by a large vertebrarterial canal. Small alar processes form the ventral lamellae. The ventral arms are larger than the dorsal and both are plugged with calcified cartilage.

SACRUM (T16). The cotyles are dorsoventrally flattened ovals. The anterior is filled with calcified cartilage to form a weakly developed condyle. This has a deep anterior pit and scarcely extends beyond the rim of the cotyle. The posterior cotyle has the lateral and ventral borders extending further posterior than does the dorsal. The antero-internal part of the cotyle is plugged with calcified tissue.

The neural canal is wide but not greatly depressed. There are relatively large spinal nerve foramina, one behind each transverse process. A low, well-developed neural crest arises at the anterior edge of the neural arch and extends posteriorly to where the arch begins to rise into the hyperapophysis. The latter ends in a long, low crest, to which the hyperapophyseal septa attach. Prezygapophyses have teardrop-shaped facets, extend anterolaterally and are strongly tilted from the horizontal. They are widely separated and extend well out from the neural arch. The facets of the postzygapophyses are more distinctly teardrop-shaped and large. They extend primarily anteroposteriorly and are dorsally concave. Zygapophyseal ridges extend from the pre- and postzygapophyses to the transverse processes. These ridges are smoothly continuous with the neural arch, which they greatly increase in lateral area.

Transverse processes are long, relatively robust, and with the arms in a single vertical plane. The arms are plugged distally with calcified cartilage and the dorsal arms are larger than the ventral. The arms are closely appressed, but separated by a narrow web of bone. Ventral lamellae are weakly and variably developed, and pierced by subcentral foramina. Vertebrarterial canals are present.

HAEMAL VERTEBRA. Cotyles are dorsoventrally flattened ovals; the anterior one containing a forwardly projecting condyle of calcified tissue. This condyle has a large pit anteriorly. The posterior cotyle has a small amount of calcified tissue anteriorly and lacks the excavation of the dorsal border seen in the trunk vertebrae. Opisthocoely is weakly developed. The haemal arch is fully developed, with a long, low haemal crest ventrally. The posterior border flares laterally and posteroventrally to produce a flattened fan, which may be weakly bicipital. A large foramen pierces one wall or the other of the haemal arch. Ventrolaterally, along each edge of the arch, are found well-developed laterally extending flanges of bone.

The neural arch is low and gently sloped laterally. A small triangular neural crest is present medially. The neural arch rises gently posteriorly to form the two processes of the hyperapophyses. A large foramen for the spinal nerve pierces each wall posterior to the transverse process and anteroventral to the postzygapophysis. Prezygapophyses are, for those of haemal vertebrae, very large. They are irregular, elongate ovals extending anterolaterally and are well set off from the neural arch, in the horizontal plane. Postzygapophyseal facets are approximately teardrop-shaped, horizontal, and dorsally concave. They are large and, like the prezygapophyses, joined by a lateral ridge of bone to the transverse processes.

The transverse processes are sometimes bicipital and sometimes merely a single vertical flange of bone extending posterolaterally. They are short and join to the interzygapophyseal ridges dorsally and to the lateral haemal ridges ventrally. A small vertebrarterial canal may or may not be present.

VARIATION ALONG THE COLUMN. *1. Condyles and cotyles*.- Anterior and posterior cotyles are dorsoventrally flattened ovals, except in the posterior caudals, in which they are circular. The anterior cotyle is filled with calcified cartilage, which extends forward to form a condyle with a large anterior depression. The vertebrae are rather weakly opisthocoelous. In the posterior caudals the centrum is amphicoelous. That is, although the anterior cotyle is almost filled with calcified tissue, it does not extend forward beyond the cotyle and has a depression anteriorly.

The posterior cotyle has calcified tissue anterointernally, but still usually retains a trace of a notochordal pit. The amount of calcified tissue in the posterior cotyle decreases posteriorly along the column. In the trunk series, sacrum, and caudosacrals the lateral and ventral rims of the posterior cotyle extend further back than do the dorsal. In the haemal series the border becomes equal all around the cotyle. The dorsal excavation of the posterior cotyle and the flat anterior surface of the anterior condyle, which have slightly expanded rims to insert just into the posterior cotyles, show clearly the strengthening and "anti-dislocation" function of opisthocoely (see below).

2. *Hypapophyseal structures*.- Subcentral keels and basapophyses are not developed, although Estes et al. (1967) claim that posterior basapophyses are present in some specimens of the genus *Salamandra*. Hypapophyseal structures are represented by haemal arches. These are long and relatively low, expanding posteriorly into a flattened, posteroventrally aligned plate. Further posterior the lateral borders of the haemal arches are developed into lateral ridges. A haemal arch is present on all caudal vertebrae.

3. *Neural crest and hyperapophysis*.- The roof of the neural arch is flattened and wide, rising posteriorly between the postzygapophyses. The lateral extent is increased by the presence of zygapophyseal ridges joining to the transverse processes. A relatively low (compare that of the newts) neural crest is present midvertebrally. This tends to be best developed in the anterior part of the trunk and decreases posteriorly to a slight degree. The crest remains low from the sacrum through much of the caudal series, but undergoes a relative increase in height and extent in the more posterior caudals.

The posterior border of the neural arch flares up and back over the postzygapophyses. This situation obtains along the column until the more posterior caudals, in which the arch does not rise posteriorly, but continues more or less horizontally into the postzygapophyses. Excepting the atlas and T1, there is relatively constant development of the hyperapophysis along the column.

4. *Zygapophyses*.- Zygapophyses have been described above for each of the kinds of vertebrae and there is little variation along the column. Zygapophyses are notable in being widely separated, large, and

connected to the transverse processes by lateral flanges from the neural arch. In the caudal series, the zygapophyses are still large and well-developed.

5. *Transverse processes*.- Transverse processes are completely lacking from the atlas. From here posteriorly they are bicipital, although those of the two trunk vertebrae anterior to the sacrum may be unicipital. The first presacral is ribless. In the trunk, transverse processes are largest on T1, with decrease in the diameter of the rib-bearers occurring posteriorly. The arms remain of approximately equal length. The distal tips of the dorsal and ventral arms tend to be in a single vertical plane. The transverse processes on the trunk vertebrae are short, not projecting far laterally. Small ventral alar processes are present anteriorly and posteriorly, as well as small vertebrarterial canals.

In the postsacrals, ribs are lacking and the transverse processes are flat and expanded dorsoventrolaterally. In the anterior part of the haemal series they may be distinctly bicipital. The processes remain until the most terminal caudals, being anteroposteriorly flattened, inclined in line with the associated myosepta, and provided with small anterior and posterior alar processes ventrally.

Pleurodeles waltli Michahelles 1830

Specimens.- One dry skeleton (UA 14368) and one cleared and stained specimen (UA 14454).

ATLAS. Anterior cotyles are small, robust structures situated largely below the level of the neural canal. Facets are oval, with the greatest diameter in the horizontal plane. The facets are slightly convex and are inclined posterodorsally and posterolaterally to some degree. The odontoid process is robust, situated midway down between the cotyles, and with a shallow, broad groove dorsally for the spinal cord. In ventral view the odontoid is somewhat similar to that of *Scapherpeton*. The posterior cotyle is flattened dorsally and, to a lesser degree, ventrolaterally. The cotyle is shallow with a flattened anterointernal plug of calcified tissue. A low longitudinal ridge is found subcentrally, which diverges anteriorly to join the anterior cotyles.

The neural canal is small and higher than wide. The arch is large and robust, especially in the area of the hyperapophysis. The roof of the arch is high and wide, rising posteriorly. Three longitudinal ridges extend along the dorsal surface: one medially and a pair dorsolaterally. There is a large foramen piercing each anterior cotyle laterally, extending medially at a slight anterodorsal angle to enter the neural canal. The hyperapophyseal area faces directly posteriorly and is composed of a pair of vertical, slightly concave facets, which rise from the tops of the zygapophyses and are very tall. Postzygapophyses are small structures attached to the posteroventral edge of the neural arch. Facets are broadly teardrop-shaped, small, and tilted laterally.

Transverse processes are lacking.

SECOND CERVICAL (T1). The anterior part of the centrum bears a large, grossly teardrop-shaped condyle, which is flattened anteriorly. This condyle does not extend far anteriorly and barely enters the posterior cotyle of the atlas. The posterior cotyle of T1 is somewhat depressed dorsally, whereas the ventral border forms a broad oval and is produced posteriorly. Calcified tissue fills the notochordal canal and forms a flat, posteriorly facing surface within the cotyle. A robust subcentral keel extends from the posterior cotyle anteriorly for about three quarters of the length of the centrum. Subcentral foramina are small and irregular in position and occurrence. Basapophyses are lacking.

The neural canal is high, formed by the walls of the neural arch rising dorsally and medially. Foramina for spinal nerves are evident anterior to the transverse processes, but none posterior, which differs from Edwards' (1976) descriptions. The arch and its associated parts are large, dwarfing the centrum. A tall, thin neural crest extends medially from the hyperapophysis to almost the front of the arch. It is not provided with an expanded bony plate dorsally (contrast *Notophthalmus*, *Euproctus*, and *Salamandrina*). Beneath the crest, the roof of the arch is notably peaked. Laterally there are horizontal flanges extending from the neural arch and connecting the transverse processes to both the anterior and posterior zygapophyses. These auxiliary flanges decrease the apparent length of the dorsal rib-bearers and increase the width of the roof of the neural arch. The robust, dorsally produced hyperapophysis extends vertically from above the postzygapophyses. Its posterior face is approximately that of a horseshoe, as in the atlas. Prezygapophyses are largely incorporated into the neural arch roof. Articular facets are small, irregular ovals, with indistinct posterior borders. Laterally they are inclined dorsally. Postzygapophyseal facets are small, ventral extensions from the hyperapophysis, in the form of irregular ovals or teardrops.

Transverse processes are robust, relatively long, and extend posterolaterally. Rib-bearers are divergent and connected by a web of bone. The arms are filled with calcified tissue, leaving the distal, articular, surfaces only slightly concave. Ventral arms are provided with small, but distinct, ventral lamellae. The dorsals are incorporated into the laterally expanded roof of the arch, excepting their distal thirds. Vertebral canals are small and irregular in position.

TRUNK VERTEBRA (T8, see Fig. 18). The anterior condyle is anteriorly flattened and dorsoventrally compressed. The posterior cotyle is excavated for the reception of the condyle of T9, with a flat anterointernal surface. The ventral border is posteriorly produced and somewhat less flattened than the dorsal border. Hypapophyseal structures are lacking.

The neural canal is small and higher than it is wide. The arch is peaked medially, with a neural crest that is concave dorsally and slopes steeply anteriorly. Webs of bone extend the roof of the arch laterally and join the postzygapophyses to the transverse processes, whereas the prezygapophyses are joined to the bony web connecting the dorsal and ventral arms by a similar flange. Small foramina for spinal nerves pierce the arch, one posteroventral to each dorsal arm of the transverse process. Between each rib-bearer and the corresponding prezygapophysis is a large cavity extending posteromedially. This is walled medially by the neural arch, dorsally by a web of bone extending posteroventrally from the prezygapophysis, and ventrally by a feebly developed alar process on the ventral rib-bearer. The hyperapophysis rises from between the postzygapophyses. Its apex is posteriorly extended with respect to the ventral portion. As in T1, there is a semi-roughened, posteriorly facing horseshoe-like surface, providing attachment for the paired hyperapophyseal muscles. Prezygapophyses are small, but less an integral part of the neural arch than in the second cervical. Facets are irregularly-shaped circles, which lie in a basically horizontal plane. Postzygapophyses are also small with irregularly-shaped circular facets, but which are raised laterally.

The transverse processes extend posterolaterally and are composed of diverging rib-bearers, which are connected by a web of bone. The ventral arms are larger than the dorsal and pierced by relatively large vertebrarterial canals medially. Ventral lamellae are absent.

SACRUM (T15). The sacrum differs from the preceding trunk vertebrae only in the hypertrophy of the rib-bearers. These extend posterolaterally and are greatly expanded distally. The dorsal arms are somewhat larger than the ventral and are slightly posterior of the latter distally. Both arms are filled with calcified tissue and have shallowly concave articular facets.

HAEMAL VERTEBRA (H3). The anterior condyle is flattened as are those of the trunk series. It is subcircular in anterior view, with the dorsal border anterior to the ventral. The posterior cotyle is also subcircular, with the dorsal and ventral borders somewhat flattened. The dorsal border is excavated anteriorly. As in the trunk vertebrae, calcified tissue plugs the chordal canal, producing a flat antero-internal surface. The haemal arch of the third haemal vertebra is completely developed, extending the full length of the centrum. The canal is notably larger than the neural canal. The haemal arch is provided with a crest and process that mirror the neural crest and hyperapophysis above.

The neural canal is small and relatively narrow, with the roof peaked above it. A well-developed neural crest is present and the hyperapophysis forms a shallow aliform process. The roof of the arch is narrower than those of the trunk vertebrae. A spinal nerve foramen is present in each wall. Prezygapophyses are small with more or less horizontal, subcircular facets, which are situated well below the roof of the neural arch. The facets of the postzygapophyses are small, teardrop-shaped, and turned up laterally. They are situated below the hyperapophysis as in the trunk region.

VARIATION ALONG THE COLUMN. *1. Condyles and cotyles.*- Throughout the trunk region the condyle projects a short distance anteriorly. In the forward part of the trunk it projects a very short distance beyond the prezygapophyses. In the rear portion the condyle ends short of the anterior edge of the prezygapophyses. Excepting that of T1 (q.v.) the condyle is dorsoventrally compressed and relatively wide. The anterior face is vertically flattened and there may be a small projection of calcified tissue in the centre of the condyle. The condyle of the single caudosacral vertebra is as that of the trunk, but more dorsoventrally compressed. The first two or three haemals possess a slightly dorsoventrally compressed condyle. However, posterior to this it forms an irregular circle in anterior view. In the haemal series the condyle is slanted such that (in lateral view) the dorsal border is forward of the ventral.

The posterior cotyle mirrors the structure of the corresponding condyle, with which it articulates. Each cotyle, excepting those of the atlas and T1 through T3, has the dorsal border excavated anteriorly, such that only the ventral and lateral borders serve to enclose the articulating condyle. The anterointernal surface of each cotyle is flattened, formed by calcified tissue. The internal surfaces of the rims are smooth, formed of bone only.

2. *Hypapophyseal structures*.- Only T1, T2, and (to a slight extent) T3 bear a subcentral keel. In these the keel is a low, thick structure occupying the middle two thirds of the centrum. On either side of the keel are dorsally excavated depressions. Basapophyses are lacking, in correlation with the lack of posterior flexures or basapophyseal muscles in the *subvertebralis*.

There is a single caudosacral vertebra. The second postsacral vertebra bears a small haemal arch. This is U-shaped and originates along the posterior two thirds to one half of the centrum ventrolaterally. No ridges or crests are developed on the first haemal arch. In the following haemals the arch occupies most of the ventral surface of the centrum, except for the area ventral to the anterior cotyle. The arch is a partial mirror of the neural arch, having a ventral haemal crest and aliform-like haemal process posteriorly. The latter are somewhat more developed than the aliform process of the neural arch.

3. *Neural arch*.- The spinal nerves exit intravertebrally throughout the column, except for the second cervical, which lacks posterior foramina in the two available specimens. In the atlas the foramina

pierce the anterior cotyles. The trunk vertebrae have the foramina located posterior to the transverse processes. The foramina of T2 are large and sometimes not enclosed posteriorly by bone. This enlargement is for the exit of a large nerve innervating the pectoral girdle. The foramina enlarge progressively from the presacrals (T11 through T14) to the sacrum (T15). Those of the single caudosacral are notably smaller than those of the sacrum. From this point posteriorly, the foramina decrease progressively in diameter.

In the atlas and T1 the small neural canal is high, with a steeply arched roof, and narrow. Its height decreases posteriorly, making the canal appear relatively wider in the midtrunk, sacral, caudosacral, and haemal vertebrae.

4. *Neural crest and hyperapophysis*.- In the atlas the roof of the neural arch is robust and provided with three longitudinal ridges. Throughout the remainder of the trunk the neural crest is a high, thin plate extending anteriorly from the hyperapophysis to approximately the level of the origin of the transverse processes. From this point, the crest slopes steeply anteriorly. In T1 the crest extends relatively further anteriorly. In the main region of the trunk the crest is concave on its dorsal margin, as is that of the caudal vertebrae.

The hyperapophysis is constant throughout the column, including that of the atlas. It rises vertically above the postzygapophyses, forming an inverted U-shape in posterior view. The rear surface of this U is relatively smooth, but with small, lateral ridges for the insertion of the hyperapophyseal septa. This species lacks the aliform-like hyperapophyses of other newts (e.g., *Notophthalmus* and *Salamandrina*), although there is a tendency for a V-shaped hyperapophysis to be present in the posterior trunk vertebrae. This tendency increases posteriorly through the haemal vertebrae, which have a shallow, but V-shaped, hyperapophysis.

5. *Zygapophyses*.- Prezygapophyses of the trunk vertebrae are constant along the column. Facets are small, often irregular circles. They extend to, or somewhat beyond the anterior edge of the condyles. Prezygapophyses are located significantly below the top of the roof of the neural arch and are supported ventrally by a strut extending anterodorsally and laterally from the centrum. The roof of the arch is slightly notched between the prezygapophyses in the anterior half of the trunk, but not in the posterior half. In the sacrum and, to a lesser degree, the first presacral the prezygapophyseal facets are somewhat teardrop-shaped (i.e., more posteriorly elongate). Facets of the caudosacral and haemal vertebrae are essentially as those of the trunk, but differ in orientation. In the trunk, facets are essentially horizontal, but in the haemals (after the first three to five) they are tipped dorsolaterally.

Postzygapophyses are essentially mirror images of the prezygapophyseal facets. However, those of the first and second postsacrals are subcircular, not conforming to the basically teardrop shape of the articulating prezygapophyses. Postzygapophyses are small, ventral adjuncts to the large hyperapophysis.

Both anterior and posterior zygapophyses are joined by laterally extending flanges of bone from the roof of the neural arch to the transverse processes. This gives them the appearance of being a much more integral part of the neural arch than is the case in other species here described.

6. *Transverse processes.*- Atlantal transverse processes are lacking. Throughout the trunk the transverse processes are long and directed posterolaterally. The dorsal arms have the true lengths obscured owing to the lateral zygapophyseal flanges. Rib-bearers are bicipital and relatively widely separated, being connected by a web of bone. They are also plugged by calcified tissue. The dorsal arms extend posteriorly at a greater angle than do the ventral, causing each transverse process to slant posterodorsally.

From T3 posteriorly there is a steady decrease in the diameter of each arm of the rib-bearers, especially in the two or three presacrals. From T5 or T6 posteriorly the articular surfaces of the dorsal arms are oriented more posteriorly than those of the ventral. In the midtrunk region the ventral arms extend nearly directly laterally for the distal one third, such that the articular surface faces laterally. However, the lateral extension is not seen in the pectoral or presacral vertebrae. Throughout the trunk posterior to the pectoral area, therefore, the articular surfaces of the dorsal and ventral arms are at different angles. The reasons for this are uncertain, but may relate to the anti-predator function of the elongate, distally sharpened ribs (see Steward 1969).

The single caudosacral has small, but distinct transverse processes, which bear ribs. The dorsal arms may be lacking. In the haemal series there is rapid decline in the size of the transverse processes. In those vertebrae posterior to the first haemal the transverse processes are perforated, amorphous projections.

Ventral lamellae are slightly developed on T1 through T3, but they are in the form of buttresses for the ventral arms, not being used as areas of muscle attachment. Excepting a small flange joining the ventral rib-bearers to the supporting column of the prezygapophyses, ventral lamellae are lacking throughout the remainder of the trunk and caudosacral regions.

Taricha Gray 1845

Specimens.- Two skeletons (UA 14373, 14374) and two cleared and stained specimens (UA 14462, 14463) of *Taricha torosa*, and four skeletons (UA 14375-14378) of *Taricha granulosa*. The vertebral columns of these species are all but identical.

ATLAS. Anterior cotyles are widely separated, laterally compressed ovals. The cotyles have flat anterior articular surfaces. Rather than extending vertically, these surfaces are tilted such that the ventral borders are anterior of the dorsal. The odontoid process is a long, narrow shelf-like extension of the centrum, which underlies the spinal cord. Two rounded facets are found ventrolaterally on the anterior edge, by means of which the odontoid articulates with the skull. The posterior cotyle is flattened dorsally and bluntly pointed ventrally. The notochordal canal is filled with calcified tissue, forming a flat surface anterointernally. The ventral border is produced posteroventrally. Two ventrolateral flanges of bone buttress the anterior cotyles to the centrum. No basapophyses are present.

The neural canal is large, and oval when viewed anteriorly. The walls of the arch are short in lateral view, arising from the centrum just posterior to the anterior cotyles. The roof of the arch is robust, with a wide, thickened boss medially. Anteriorly the dorsal part of the arch flares up and forward into a thin flange, which sends a short median projection posteriorly over the median boss of the neural arch. In dorsal view the flange and the posterior projection form a T-shaped structure. The rear of the neural arch is heavy and provided with a posteriorly facing pair of facets. Postzygapophyses originate on the posterolateral sides of the hyperapophyseal area and extend well back of the arch. Articular facets are approximately comma-shaped, the narrow tip extending anteriorly. The lateral edges of the facets are raised and the whole facet is tipped posterodorsally.

There are no transverse processes.

SECOND CERVICAL (T1). The condyle is flattened anteriorly, with the dorsal border forward of the ventral. A rim extends around the condyle, which articulates with the posterior cotyle of the atlas. The cotyle of T1 is oval in the horizontal plane, with the dorsal rim flattened and excavated anteriorly. Anterointernally a flat surface formed by calcified tissue plugs the centrum. The walls of the cotyle are free from infilling. No hypapophyseal structures are evident, except for a tendency to develop a low transverse ridge posteroventral to the condyle. Subcentral foramina are of irregular distribution in the ventral lamellae.

The neural canal is large, approximately a pentagonal shape anteriorly, and the roof of the arch is strongly inclined. A small foramen pierces the arch immediately anterior to the origin of each dorsal rib-bearer. Posteriorly, a large foramen may be blocked off by a posterior strut of bone, although the spinal nerves are usually not enclosed in bone here. A high, dorsally flat neural crest extends the length of the arch from the hyperapophysis to almost the front of the arch. The hyperapophysis is high, in the form of a shallow aliform process above the postzygapophyses.

Prezygapophyseal facets are small, irregularly shaped circles, situated well below the roof of the arch, and extending a short distance anterior of the arch. They are strongly tilted and extend dorsolaterally. Postzygapophyses are smaller than the prezygapophyses and in the form of highly irregular ovals or circles. They are weakly inclined from the horizontal and shallowly concave. Zygapophyses are joined by horizontal, lateral flanges to the transverse processes, thereby greatly increasing the width of the roof of the arch.

Transverse processes are robust and relatively long. They proceed laterally and slightly posteriorly and are bicipital. The arms are plugged by calcified tissue and joined by a bony web, but are not widely separated or divergent. The ventral arms are expanded proximally to form robust, ventral lamellae. Ventral lamellae blend with the centrum to form a shallow basin in ventral view. A tiny vertebrarterial canal pierces each ventral rib-bearer.

TRUNK VERTEBRA (see Fig. 19). The anterior condyle extends forward to articulate with the cotyle of the preceding vertebra. The head is expanded and its anterior surface is flattened. The posterior cotyle is flat dorsally and the lateral and ventral edges form a laterally elongate oval. The notochordal area is filled with calcified cartilage, forming a flat surface anterointernally. The dorsal rim is excavated anteriorly, leaving a more extended rim laterally and ventrally to surround the condyle of the following vertebra. This contrasts to lizards, snakes, and *Desmognathus*, in which there is a true ball-and-socket developed between each vertebral pair. A subcentral keel is lacking, the centrum being dorsally concave in lateral view. Basapophyses are absent, but there are several irregularly shaped and spaced subcentral foramina.

The neural arch is low. A tall neural crest arises at the posterior border of the prezygapophyseal facets. It rises sharply and then continues to rise gently to the top of the hyperapophysis. A shallow aliform process forms the hyperapophysis. In posterior view there is a triangular-shaped facet for the insertion of muscles on the hyperapophysis. Prezygapophyseal facets are elongate ovals, extending anterolaterally. The lateral borders are deflected dorsally, the orientation of the facets in anterior view being dorsolateral. Prezygapophyses are strongly buttressed to the arch, the roof extending well forward between them and there is a posterior ridge extending from the anterior surface of the dorsal rib-bearer to the prezygapophysis on either side of the vertebra. Postzygapophyses have lateral flanges extending forward to the transverse processes. Articular facets are teardrop-shaped and disposed anteroposteriorly with a slight lateral displacement posteriorly. Facets are inclined from the horizontal so as to meet the prezygapophyses of the following vertebra.

Well-developed, although short, transverse processes are present. They originate just anterior to the midpoint of the centrum and extend posterolaterally at a relatively sharp angle. The two arms are close together, parallel, and both are located in a single vertical plane. The arms are tubular, but filled with calcified tissue. First and second alars are present, the first (posterior) more extensively developed than the second. There are small vertebrarterial canals piercing the ventral rib-bearers.

SACRUM (T14). The sacrum is basically as the trunk vertebra just described. The transverse processes are much more robust, with the ventral arms ending in flattened ovals and the dorsal arms subcircular. The first alar processes are less extensively developed than in the trunk vertebrae. The condyle is less anteriorly extended and is a more rounded ball.

HAEMAL VERTEBRA (H3). The condyle and cotyle are as in the trunk vertebrae. A well-developed haemal arch is present, extending anteriorly and posteriorly along the underside of the centrum to almost the same length as does the neural arch dorsally. A haemal crest is developed subequally to the neural crest and a similar aliform process is present.

A high, long neural crest rises dorsally from the level of the posterior edges of the prezygapophyseal facets and then proceeds posteriorly to the hyperapophysis. A relatively well-developed aliform process is present, but filled with "spongy" bone. The neural arch does not extend behind the postzygapophyses. Zygapophyses are more or less developed as in the trunk region.

Transverse processes are each a bulbous mass of bony tissue, pierced by numerous holes.

VARIATION ALONG THE COLUMN. *1. Condyles and cotyles.*- The condyle is formed by a short neck of calcified tissue protruding from the anterior cotyle and bearing an expanded cap anteriorly. This cap is relatively flat anteriorly, but with some curvature. The dorsal portion of the condyle is in advance of the ventral in the middle and posterior parts of the trunk. In the anterior trunk region the cap has a more or less vertical anterior face, as is the case in the haemal series. The condyle is otherwise little differentiated along the column.

The cotyle is flattened and excavated dorsally. The lateral and, especially, the ventral edges are thus situated further posteriorly. The notochordal canal is filled with calcified tissue so as to form a flat wall anterointernally. The cotyle is dorsoventrally compressed throughout the column, becoming more rounded in the haemal series. The most posterior caudal vertebrae are amphicoelous.

2. Hypapophyseal structures.- Hypapophyseal structures are lacking. A haemal arch is present from the third postsacral vertebra posteriorly. The arch is robust and well formed, with a long crest and posterior aliform process. The haemal arch comes to mirror the neural arch complex above.

3. Neural crest and hyperapophysis.- The neural crest is present throughout the column. That of the atlas is robust, wide, and low, but in the rest of the column the crest is a tall, thin, medial sheet of bone along most of the length of the neural arch. It is high in the vertebrae of the pectoral region, then decreases steadily to the sacrum. Postsacrally there is an immediate increase in height, which is maintained through the caudal series.

The hyperapophysis is in the form of an aliform process. This is not developed on the atlas and is poorly developed in the vertebrae associated with the pectoral girdle. The V increases in size posteriorly, to be most strongly developed in the caudal series. The arms of each aliform complex serve as a site of insertion for hyperapophyseal septa.

4. *Zygapophyses*.- Zygapophyses are present with little variation until the most posterior ten or so caudal vertebrae. They are generally developed as in the trunk vertebrae (described above).

5. *Transverse processes*.- T1 has well-developed, bicipital, slightly divergent rib-bearers joined by a web of bone. The second trunk vertebra is much the same, but the dorsal arms are somewhat larger than the ventral and set further posteriorly. Posteriorly, the rib-bearers, although remaining bicipital, become closely appressed and progressively of smaller diameter. The two arms remain in more or less the same plane and extend posteriorly at about the same angle throughout the trunk. The first two postsacral vertebrae have bicipital transverse processes, but the dorsal arms are weak.

The posterior alar processes are constantly developed throughout the column. Anterior alar processes are present on transverse processes of the midtrunk region, and in the postsacrals. In the haemal series, the transverse processes become amorphous, sponge-like lateral projections on the centra. These projections are present to almost the end of the tail.

Notophthalmus viridescens (Rafinesque 1820)

Specimens.- Four skeletons, both sexes, of adults (UA 14369-14372); one cleared and stained metamorphosed adult (UA 14456); three cleared and stained neotenes (UA 14455, 14457, 14458); and three cleared and stained larvae (UA 14459-14461).

ATLAS. In overall form the atlas is very like that of *Triturus*, differing mainly in the neural crest and hyperapophysis. Anterior cotyles are small and subcircular, with the dorsal and lateral edges inclined posteriorly. Articular facets are gently convex and situated on the ventrolateral borders of the neural canal. The odontoid process is long, wide, and thin. In anterior view it is a dorsally concave crescent situated medially with respect to the anterior cotyles and it has a pair of well-developed ventrolateral facets. The posterior cotyle is approximately egg-shaped, the broadest part dorsal. There are no projections from the rim. The cotylar cup is shallow, being filled anterointernally with calcified tissue to form a flat surface. Hypapophyseal structures are lacking.

The neural canal is large, roughly triangular in anterior view, and with basal internal projections from each side of the neural arch. The arch arises from almost the entire length of the centrum and also from the dorsolateral part of each anterior cotyle. Immediately behind each cotyle is a large spinal nerve foramen. Behind each foramen a low, robust ridge runs along the side of the neural arch. This ridge and the lateral edge of the anterior cotyle form two parallel rows, between which the foramen opens. The neural crest is a wide, low anterior continuation of the hyperapophysis. The latter is a tall, heavy structure with a pair of vertical, posterolaterally directed flanges, forming a shallow aliform process. This process encloses a posteriorly directed double facet, each half of the pair arising from above a postzygapophysis. Postzygapophyseal facets are long teardrops, positioned anteroposteriorly, and with the lateral edges upturned. Excepting the low lateral ridges on the arch, transverse processes are lacking.

SECOND CERVICAL (T1). The anterior condyle extends relatively far in front of the centrum. It is circular in anterior view, with a flat forward surface, and a low rim extending round the anterior circumference. Posteroventral to the condyle a small process extends anteroventrally from the centrum. The posterior cotyle is dorsoventrally compressed with a flattened dorsal surface and a shallow cotylar cup. The anterointernal surface is flattened and the rim is smooth. A low, robust hypapophyseal keel runs the length of the centrum, and extends somewhat forward and ventrally, as a wide spur beneath the posterior edge of the anterior condyle. Basapophyses are lacking.

The neural canal is large and subcircular in end view, with the arch gently expanded above. A large spinal nerve foramen pierces each wall of the arch, entering into the post-transverse process recess (see below). The neural crest is tall and robust, extending almost the full length of the roof of the arch, and forming a rectangle in lateral view. The dorsal edge is expanded laterally in larger metamorphosed adults, with a flattened, rough dorsal surface. The hyperapophysis is developed as an aliform process with a very shallow, posteriorly facing, V-shaped facet. The facet is very like that in *Siren*, but of less forward extent and with a posterior ridge running vertically along the median internal part. Prezygapophyseal facets are anteroposteriorly extending, elongated ovals with the anterolateral edges somewhat inclined. They are pressed against the sides of the neural arch and extend only slightly past the forward border of the roof of the arch. Postzygapophyseal facets are approximately diamond-shaped, positioned posterolaterally, and with the lateral edges raised. A prominent lateral ridge extends from the roof of the arch, joining the anterior and posterior zygapophyses on either side.

Transverse processes are robust, short and bicipital, but not divergent. They extend posterolaterally and have a slight ventral deflection. A small, robust ventral lamella lacking subcentral foramina is present on each ventral rib-bearer proximally. A rim of bone extends from each ventral lamella dorsally along the distal end of the transverse process. Above the ventral lamella, the transverse process is excavated by a large posterior hole, which here is termed the post-transverse process recess. The foramen for the spinal nerve opens into this hole.

TRUNK VERTEBRA (T7, see Fig. 19). The anterior condyle is large with its face gently rounded. In anterior view it appears as a rounded triangle stood on the apex. The dorsal part extends further forward than the ventral, causing the condyle to be sloped in lateral view. The posterior cotyle is large, subcircular, and with a flattened dorsal surface. The cup is shallow, with a flat anterointernal surface formed of calcified tissue. A low, robust subcentral keel runs the length of the centrum and a short, wide flange extends beneath the anterior condyle. Small, irregular subcentral foramina are present on either side of the subcentral keel. Basapophyses are lacking.

The neural canal is a large, approximately pentagonal opening in anterior view. The roof of the arch is domed and anteriorly almost covers the condyle in dorsal view. A small spinal-nerve foramen pierces each wall inside the post-transverse process recess. The neural crest is robust, high, and rectangular, extending most of the length of the roof of the arch. The dorsal surface of the crest is flat, roughened, and laterally expanded. A shallow aliform process occupies the hyperapophyseal area. Prezygapophyseal facets are teardrop-shaped, positioned anterolaterally and situated against the sides of the neural arch. Only a small fraction of each prezygapophysis extends beyond the anterior edge of the arch. The lateral edges of the facets are slightly raised. Postzygapophyseal facets are broad teardrops, extended anteroposteriorly, and situated more or less horizontally. A lateral flange joins the anterior and posterior zygapophyses on either side, greatly widening the neural arch roof.

Transverse processes are short and robust. They are distinctly bicipital, but the arms are parallel to each other. The ventral arms arise from just behind the anterior condyle, the dorsal from the centre of the neural arch. Both arms extend posterolaterally, but as the dorsal arms are posterior to the ventral, each transverse process is tipped from the vertical. Ventral lamellae, similar to those in *Siren*, are developed on each ventral rib-bearer. Anterior alars join the ventral arms to the centrum, and extend forward as projections posterolateral to the condyle. Small posterior alars are present in the angles formed by the ventral arms with the centrum. Midway along each transverse process an irregular spur of bone projects posteriorly. Its occurrence is irregular, certain vertebrae lack it on both sides, some have it on one side or the other, and others have it on both transverse processes. The spur correlates with the insertion of subvertebral musculature. Medial to the spur the post-transverse process recess is formed, an anteriorly directed excavation between the arms of the transverse process and next to the centrum.

Although small, trunk vertebrae are very compact and robust.

SACRUM. The sacrum scarcely differs from the trunk vertebra described. There is no subcentral keel and subcentral foramina are of irregular shape and location. The neural crest is high, but relatively short and the top is not expanded. The transverse processes are markedly expanded in comparison to those of the presacrals, but not with respect to the more anterior trunk vertebrae. Rib-bearers are in a single vertical plane and the dorsal arms are of larger diameter than the ventral arms.

HAEMAL VERTEBRA (H4). There is only a single caudosacral vertebra, as a haemal arch appears on the second postsacral. The anterior condyle projects rather far in front of the centrum, with the dorsal part extending further than the ventral. The condyle is well formed, subcircular in anterior view, with a small rim and gently convex anterior surface. The posterior cotyle is large, subcircular, and flattened dorsally. The cotylar cup is shallow with a flat anterointernal cartilage plug. The ventral rim extends posteriorly. The haemal arch basically mirrors the neural arch, but with a larger canal, a longer haemal crest, and without zygapophyses. A well-developed foramen pierces the wall of the haemal arch just posterior of the midpoint on either side.

The neural canal is fairly large and bean-shaped in anterior view. The roof of the arch is gently domed and there are small foramina for the spinal nerves, one on either side, recessed into depressions posterodorsal to the transverse processes. The neural crest is thin, tall, and arises from the posterior three quarters of the roof of the neural arch. The anterior edge slopes ventrally in a convex pattern from the top of the hyperapophysis to the roof of the arch. An aliform process with short wings rises above the postzygapophyses, to the top of the neural crest, so as to enclose a shallow, posteriorly facing V-shaped facet. Prezygapophyseal facets are elongate, anterolaterally extending ovals with the lateral edges irregular ovals, disposed anteroposteriorly, and situated horizontally. A laterally extending flange joins the zygapophyses on either side.

Transverse processes are thick, robust wing-like structures extending laterally from the side of the centrum. The posterior edges are flat and each process thins anteriorly, producing a triangle in para-sagittal section. There are no vertebrarterial canals.

VARIATION ALONG THE COLUMN. 1. *Condyles and cotyles*.- The condyle is anteriorly flattened with the forward part gently rounded. A raised rim is present around the condyle, set off by a posterior neck. In T1 the condyle is subcircular, and slightly higher than wide. That of T2 is circular in anterior view, but that of the following trunk vertebrae is a dorsoventrally compressed oval. Behind the pectoral area, the dorsal edge of the condyle tends to be flattened, while the ventral is more rounded. In the two or three presacral vertebrae and in the sacrum the condyle is more pronounced and laterally elongate. Caudosacrals and the first two or so haemals have a condyle formed as in the trunk, although smaller. In the remainder of the caudal region the condyle is circular, with a tendency to be higher than wide.

Throughout the column, the condyle has the anterior face at an angle when viewed laterally, such that the dorsal rim is anterior to the ventral. This is especially evident in the trunk vertebrae between the two limb girdles. Posterior to the condyle a ventral flange extends laterally and projects somewhat forward. This is best developed in T1, from which point it gradually decreases in size. It is present on all trunk vertebrae, but is lacking from the sacrum and the caudosacrals (compare *Triturus vulgaris*).

The posterior cotyle reflects the shape of the condyle, with which it articulates. The cavity is shallow with a flattened anterointernal surface. Throughout the column, but especially in the trunk and haemal vertebrae, the ventrolateral and ventral rim of the cotyle is posteriorly extended.

2. *Hypapophyseal structures*.- The ventral flange found in association with the condyle has been noted. A low, robust subcentral keel is present on the immediately postpectoral vertebrae (about T4 through T9). The other trunk vertebrae tend to lack this keel or have it only

faintly developed. It is most evident in large individuals. Other than this, hypapophyses and basapophyses are lacking.

A small, weak haemal arch is developed on the second postsacral vertebra. This structure increases progressively in size and elaboration until, by H4, it is fully developed. The haemal arch comes to mirror the neural arch, and has a haemal canal that is higher than wide. A well-developed haemal crest extends ventrally, much further than does the neural crest dorsally. A haemal aliform process occurs posteriorly, mirroring the aliform process of the neural arch above. This structure is present posteriorly to the most posterior few caudals.

3. *Neural arch.*- The neural canal is large and high in T1. Posteriorly, it becomes progressively smaller and lower. In the midtrunk region it is somewhat wider than high and the roof is arched above the canal. Presacrals and the sacrum show increase in the size of the canal, which then progressively decreases in size. In the sacral and postsacral region the canal is about as high as wide, and gently rounded dorsally. *Notophthalmus* lacks the lateral crests associated with the zygapophyses that widen the roof of the neural arch in other newts (especially *Triturus vulgaris* and, to a lesser degree, *Taricha*). The arch is not excavated between the anterior zygapophyses.

4. *Neural crest and hyperapophysis.*- The neural crest is a tall, robust plate with a vertical anterior border and a flat dorsal border. It extends almost the entire length of the neural arch. Dorsally, the crest is capped by a rugose, laterally expanded plate, especially well-developed in the pectoral region, but present back to the presacral area in larger individuals. The plate is lacking behind the

sacrum, although the neural crest undergoes an increase in height in the first part of the caudal series. This plate is only seen in metamorphosed adults.

A well-developed, high aliform process is present throughout the column. It is relatively shallow, however, and capped dorsally by a posterior continuation of the dorsal plate of the neural crest. The high neural crest and aliform process are associated with the hyperapophyseal muscles, which arise on the lateral edge of each neural crest and extend anteriorly to the posterior, vertical rim of the aliform process of the next anterior vertebra. The dorsal plate does not, however, serve for attachment of trunk musculature, presumably being a defensive structure.

5. *Transverse processes*.- Excepting T1 through T3, the two presacrals, and the sacrum, the transverse processes are of relatively constant development in the trunk. They are bicipital with gently diverging arms and located below the level of the zygapophyses (contrast *Triturus vulgaris*). The rib-bearers of the anterior vertebrae (T1 to T3) are conspicuously more robust than those of the other vertebrae. Presacrals lack the dorsal arms, but a high flange extends dorsally and slightly posteromedially from the ventral arms. All vertebrae up to and including the sacrum have small, but robust, posterior or posteromedial projections from the webbing that connects the rib-bearers. The transverse processes slant dorsally in a posteromedial direction. Distinct ventral lamellae are present throughout the trunk. Posterior to T2 these project forward in a manner foreshadowing the condition of *Siren* (q.v.).

The single caudosacral vertebra has robust transverse processes and ventral lamellae. Only the ventral rib-bearers are present, bearing thick, low ridges on their dorsal surfaces. The first haemal has robust, unicipital transverse processes with distinct ventral lamellae and small dorsal ridges. There is progressive, gradual decrease in the transverse processes posteriorly. Posterior to H4 or H5 the transverse processes are short, but elongated antero-posteriorly. Traces of these processes are present until the most posterior areas of the tail.

Very small, often multiple, vertebrarterial canals pierce the ventral rib-bearers throughout the trunk.

6. Zygapophyses.- Prezygapophyses are relatively small, lateral extensions of the wall of the neural arch. They increase in size posteriorly from the second cervical and also come to be more pronounced and laterally raised. Facets are elongate ovals (sometimes almost teardrop-shaped), which are positioned anterolaterally. Dorsolateral deflection of the facets is most marked in the midtrunk region, and decreases anteriorly and posteriorly.

Postzygapophysis mirror the prezygapophyses. Zygapophyses are present until the posterior third or quarter of the caudal series.

Triturus vulgaris (Linnaeus 1758)

Specimens.- Six skeletons (UA 14384-14389) and eight cleared and stained specimens (UA 14472-14479).

ATLAS (see Fig. 20). Anterior cotyles are somewhat more widely separated than in *Triturus cristatus*. Facets are subcircular, but quite variable in shape. In contrast to those of *T. cristatus*, which are wider than high, the facets are slightly higher than wide. The articular surfaces are small and flat, located ventrolateral to the neural canal. The odontoid process is relatively shorter and narrower than in *T. cristatus*. It is thin and gently concave dorsally, for the passage of the nerve cord. Less of a neck is developed posteriorly and the ventrolateral facets are relatively larger than in *T. cristatus*. The posterior cotyle is small and subcircular, tending to lack the dorsal flattening seen in *T. cristatus*. The rim is generally level, although there may be a ventral extension in some individuals. The cotylar cup is deep and the chordal area is plugged with calcified tissue, forming a flat anterointernal surface. Basapophyses are lacking and the ventral surface of the centrum is smooth, although irregularly pierced by small subcentral foramina.

The neural canal is a large diamond-shaped opening. The arch is basically as in *T. cristatus*, but with several modifications. The walls are somewhat longer, and the roof of the arch lacks a low, thickened boss. The hyperapophyseal area rises dorsally, but is excavated by a shallow notch. Spinal nerve foramina pierce the anterior cotyles through the posterodorsal margins. Postzygapophyses are small, elongate ovals or teardrops, but are much less anteroposteriorly extended than in *T. cristatus*. The lateral borders are raised.

Transverse processes are absent, but a lateral flange is present on the anterior part of the neural arch, just behind each anterior cotyle.

SECOND CERVICAL (T1). The front of the centrum is provided with a well-developed, rounded condyle of granular calcified tissue, subcircular in anterior view. Posterior to the condyle is a ventral projection from the centrum. The posterior cotyle is subcircular and slightly wider than high. The cotyle is deep and lacks infilling along the internal walls, whereas the chordal area is plugged by calcified tissue. Smaller specimens tend to have a pair of large, irregular subcentral foramina. Larger individuals have the ventral surface of the centrum solid and smooth, as in *T. cristatus*. Excepting the anterior projection, hypapophyseal structures are not developed.

The neural canal is large, about as wide as high. The canal is squarish in anterior view, but with the roof gently arched. The large size of the neural canal gives the vertebra a relatively high, "chunky" appearance, in contrast to the lower, more elongate second cervical of *T. cristatus*. With the presence of lateral flanges joining the zygapophyses to the transverse processes, the former are more or less incorporated into the roof of the arch, which, therefore, resembles a rectangle in dorsal view. The roof is not excavated between the prezygapophyses, but extends anterior to or almost to the anterior edges of the zygapophyses.

The neural crest is a thin, dorsally produced plate rising above the aliform process and ending anteriorly just behind the edge of the roof of the neural arch. The hyperapophysis is developed into a small, but distinct, aliform process. At its apex is a vertical flange. No true floor (as in *Siren*) to the aliform process is present, although in larger individuals a small, posteromedial flange underlies each of the arms of the aliform process. A very small foramen pierces the arch wall anterior to the origin of the dorsal rib-bearer on either side. In contrast to *T. cristatus*, the large posterior pair of foramina are lacking, although the arch may be slightly excavated posteriorly, just above the centrum.

As noted, prezygapophyses are incorporated into the neural arch. They lack auxiliary supports and buttresses. Facets are small and of variable shape, being teardrops, ovals, or subcircular. Postzygapophyseal facets are vaguely teardrop-shaped, positioned anteroposteriorly with the lateral borders tilted upwards.

Transverse processes are relatively longer and more robust than in *T. cristatus*. They are bicipital with a web of bone joining the arms out to the distal tips. The transverse processes originate just anterior of the midpoint of the neural arch. Ventral arms attach to the centrum by means of thick ventral lamellae and extend posterolaterally in the horizontal plane. Dorsal arms are of greater diameter than the ventral ones. They extend posterolaterally and dorsally from the walls of the arch. In some specimens a low flange is found along the posterodorsal surface of the dorsal arm. This extends dorsally and joins to the neural arch medially.

TRUNK VERTEBRA (T8, see Fig. 21). The anterior condyle is robust, projecting to the anterior edge of the prezygapophyses. The condyle is a dorsoventrally compressed oval. In larger individuals the anterior face is rounded, whereas smaller specimens have it flattened. The posterior cotyle is also dorsoventrally compressed, lacking infilling, and with the chordal plug relatively far forward. The dorsal rim is somewhat flattened and slightly excavated. Several irregular subcentral foramina are present. Hypapophyseal structures are lacking, notably the anteroventral projection described in T1.

The neural canal is smaller (proportionally and absolutely) than that of the second cervical. The canal is wider than high and the roof is swollen above. Well-developed lateral flanges connect the zygapophyses to the transverse processes, but to a lesser extent than in T1. The neural crest is plate-like, extending to the level of the top of the aliform process, which is well developed and relatively high. This lacks a floor (contrast *Siren*) in smaller individuals, but larger ones have longitudinal flanges on the inner walls of the aliform process, or a small floor anteriorly. Spinal nerve foramina pierce the walls of the arch just behind the origin of the transverse process on either side. Prezygapophyseal facets are similar in shape to those of *T. cristatus*, but somewhat less elongate. They are incorporated into the neural arch and barely extend beyond the front of it. They are slightly raised laterally and extend from the wall of the arch. Postzygapophyseal facets are more or less horizontal, wide posteriorly, and elongate anteroposteriorly. The forward part is narrower than the posterior and the facet may or may not be teardrop-shaped.

Transverse processes are well developed and distinctly bicipital with a web of bone joining the arms. The dorsal arms are longer, extend somewhat further posteriorly, and rise posterodorsally in contrast to the ventral. The ventral arms are provided with well-developed ventral lamellae, which arch anterolaterally. The web of bone joining the rib-bearers has a single posteriorly projecting spike on either side, correlating with the insertion of a block of subvertebral muscles (q.v.). No vertebrarterial canal is evident.

SACRUM. Of the available specimens of metamorphosed individuals (adult and subadult) one had T15 as the sacrum, in nine T14 was the sacrum, and one had T13 as the sacrum. Of the available larvae, all had T14 as the sacrum. Except for the increase in diameter of the rib-bearers, the sacrum is as the presacral trunk vertebrae.

The condyle is a slightly rounded, dorsoventrally compressed oval, with a small, but distinct, neck behind the head. The posterior cotyle is, as in the trunk series, oval, with slight excavation of the dorsal and, to a lesser extent, the ventral rims. A pair of subcentral foramina is usually present. There is no hypapophysis, the ventral surface being smooth from condyle to cotyle.

The neural canal is large, but not significantly larger than those of the presacrals. The arch is slightly swollen and the lateral flanges joining zygapophyses to transverse processes are well developed, producing a rectangular roof. The neural crest is large, as high or higher than the top of the aliform process. The latter is as in the trunk series. Foramina for the nerves are not notably larger than those of the preceding trunk vertebrae. They pierce the walls of the arch immediately behind the transverse processes and open almost directly posteriorly. Prezygapophyses are more distinct from the arch than in the trunk series. Facets are anterolaterally elongate ovals, narrowing somewhat posteriorly. They originate about a third of the way down the neural arch wall and are tilted dorsolaterally.

Postzygapophyseal facets are of variable shape, being irregular circles or broad teardrops. They are less elongate than the prezygapophyseal facets, but correspondingly inclined.

Transverse processes differ from those of the trunk region in the marked increase in the diameter of the rib-bearers. Ventral lamellae are present, although less anteriorly projecting in comparison to those of the presacrals. Posterior projections from the bony webs seem to be lacking, as they are from the presacrals.

HAEMAL VERTEBRA (H3). The condyle is gently rounded and slightly compressed dorsoventrally. The cotyle is subcircular with the dorsal rim somewhat flattened. Infilling is lacking, but calcified tissue plugs the chordal area. The haemal arch is an approximate image of the neural arch, but lacks analogues of the zygapophyses. The haemal canal is circular in anterior view and small. The haemal crest is deeper and shorter than the neural crest. The haemal process is long, forming an aliform process similar to, but larger than, that of the neural arch. A lateral crest curves anterodorsally from the lateral edge of the haemal aliform process to join with the ventral edge of the transverse process on each side of the vertebra.

The neural canal is of average size, approximately as wide as high. The roof of the arch is gently, but distinctly, swollen medially. As in the more anterior vertebrae, the lateral flanges connecting the zygapophyses to the transverse processes are well developed. The neural crest is high and plate-like, extending forward to the level of the prezygapophyseal facets. The anterior border of the crest slopes posteriorly. The hyperapophysis extends into a high, shallow aliform process, which in larger specimens has a small floor developed anteriorly. Foramina for the exit of spinal nerves are not always present on both sides of the arch. Prezygapophyseal facets are long ovals, which are narrower posteriorly than anteriorly. They are raised laterally and extend anterolaterally. Postzygapophyseal facets are elongate, irregular ovals, positioned anteroposteriorly with little displacement from the horizontal.

The transverse processes are deep, short, plate-like extensions from the centrum and walls of the neural and haemal arches. These plates proceed posterolaterally, are smooth anteriorly, and attach to the centrum posteriorly by a honeycomb of bone.

VARIATION ALONG THE COLUMN. *1. Condyles and cotyles.*- The condyle of T1 is circular and anteriorly rounded, with a ventral and ventrolateral flange posterior to it. This flange perhaps functions to restrict movement of the atlas on the second cervical. None of the remaining vertebrae have this flange associated with the condyle. The condyle of the following trunk vertebrae is dorsoventrally compressed. Except for the final two or three presacrals, which are compressed dorsoventrally, the trunk vertebrae from T4 on have only the dorsal border of the condyle compressed.

In the presacrals, sacral, caudosacrals, and haemals the condyle is compressed dorsoventrally. In the haemal vertebrae the condyle is somewhat rounded ventrally, however.

The shape of the posterior cotyle reflects that of the corresponding condyle. No infilling is evident, but the chordal foramen is plugged. The cotylar cup is deep, with a flattened anterointernal surface and excavation of the dorsal rim.

2. *Hypapophyseal structures*.- Hypapophyseal structures in the form of subcentral keels and basapophyses are lacking. In the tail, a haemal arch is present. The second postsacral vertebra has a simple ring of bone posteriorly, representing the first haemal arch. This is progressively elaborated through H2 and H3. From here posteriorly, the arch is fully developed and extends most of the length of the centrum. The haemal canal is large and approximately triangular in anterior view.

A large haemal crest, similar to the neural crest above, is present, but it extends anteriorly to the edge of the haemal arch. A distinct aliform process is present at the rear of the crest. Lateral flanges extend anterodorsally from the lateral edges of the haemal aliform process to the bases of the transverse processes. Midlaterally, a large foramen pierces each haemal wall.

3. *Neural arch*.- The neural canal is large throughout the column. In the middle of the trunk it is somewhat wider than high. The first few trunk vertebrae have an enlarged, high neural canal, but there is no marked increase in the sacral region, in contrast to most other salamanders. In the haemal series the neural canal decreases in size, but retains the same general configuration as in the trunk.

The neural arch is gently swollen, especially between the prezygapophyses. In dorsal view the roof of the arch appears rectangular, owing to incorporation of the zygapophyses into the neural arch and the development of lateral flanges connecting them to the transverse processes. These zygapophyseal crests are especially well developed in the sacral area.

The spinal nerves exit intravertebrally. Foramina in the atlas and T1 have been described. In T2 these foramina are variable: a single large foramen on either side; a double foramen; or a simple posterior notch cut in the neural arch may be present. This results in a vertebra often having different situations in either wall. Nevertheless, the exits are always posterior of the transverse processes, as is the case in the remainder of the column.

4. Neural crest and hyperapophysis.- The crest is of typical newt form: a high, relatively thin plate extending most of the length of the neural arch. It is not as high as in some other newts (e.g., *Notophthalmus*), but does bear a flattened plate dorsally. In the postpectoral region the crest is lower, but there is increase in height in haemal vertebrae. The dorsal surface of the crest is generally horizontal, running forward from the top of the aliform process. In the haemals, the crest is shorter and somewhat higher.

A well-developed, relatively shallow aliform process forms the hyperapophysis along the column. In the atlas and first two or three trunk vertebrae an irregular, vertical flange is present in the apex of the aliform process. Posterior to these, there is a short, shelf-like projection ventrointernally under the aliform process. This shelf drops out in the sacral region, but is partially developed in the haemal series.

5. Zygapophyses.- Prezygapophyseal facets are teardrop-shaped and large. They are strongly tilted dorsolaterally in the first few trunk vertebrae, but become almost horizontal in the midtrunk region. Postsacrally there is a slight increase in dorsolateral inclination of these facets. Postzygapophyseal facets tend to be teardrop-shaped, with their size, shape, and orientation reflecting that of the prezygapophyses with which they articulate.

6. Transverse processes.- Throughout the trunk the ventral rib-bearers are short and of lesser diameter than the dorsal. Rib-bearers are relatively short and extend posterolaterally, with the dorsal arms situated posterior to the ventral. This causes the distal edges of the transverse processes to slant posterodorsally in lateral view. Ventral rib-bearers extend posterolaterally and horizontally, whereas the dorsals extend posterodorsolaterally, thus producing distinctly bicipital transverse processes. The rib-bearers are connected by a web of thick bone, which extends a short distance beyond the distal ends of the dorsal and ventral arms throughout the trunk.

The diameter of the arms of the transverse processes decreases from T1 up to the sacrum. The arms in the presacral region are of small diameter. Posterior to the pectoral girdle the bony web between the rib-bearers has a posteriorly projecting spike distally. This spike becomes small in the presacrals and is lacking from the sacrum, caudosacrals, and haemals. Muscle fibers originate on the anterior face of one transverse process and converge anteriorly onto the spike (see below).

The single caudosacral has unicipital transverse processes with only the ventral arms developed, although not bearing ribs. A well-developed plate extends posterodorsally from this "rib-bearer."

Ventral lamellae are present on all trunk vertebrae, although they are less extensively developed on T1, T2, and the sacrum. The caudosacral has a large, flat ventral lamella on either side, presumably owing to the presence of the cloaca. The ventral rib-bearers are generally pierced by a very small vertebrarterial canal.

Triturus cristatus (Laurenti 1768)

Specimens.- Eleven skeletons (UA 14392-14402) and five cleared and stained specimens (UA 14481-14485).

ATLAS. The anterior cotyles are close together, with their dorsolateral edges inclined posteriorly. Articular facets are irregular circles, varying somewhat from specimen to specimen, and sometimes from side to side on a single individual. The surfaces are flat, relatively small, and positioned beneath the neural canal. The odontoid process is small, but well developed. It is long and narrow, thin and dorsally concave, and located approximately midway down between the cotyles. There are two ventrolateral facets, which join to the inner surfaces of the occipital condyles. The posterior cotyle is small and subcircular, but with the dorsal edge slightly flattened. The cup is deep and infilling absent, although the chordal area is plugged anteriorly, forming a flat surface. Basapophyses and hypapophysis are lacking.

The neural canal is a large, dorsoventrally flattened oval in anterior view. The neural arch arises from the posterior parts of the anterior cotyles and the dorsolateral walls of the centrum, and extends dorsomedially. Spinal nerve foramina pierce the neural arch and anterior cotyle, one on either side. Just behind each foramen is a flange along the external surface of the arch. The neural crest is represented by a low ridge running the length of the roof of the arch. The roof is thickened on either side of the crest so as to produce a low, rough boss. The roof is not excavated posteriorly as in other *Triturus* (i.e., *T. alpestris*, *T. marmoratus*, *T. vittatus*, and *T. vulgaris*). The hyperapophysis is provided with a pair of complex, posteriorly facing facets, each rising dorsally and slightly medially from one of the posterior zygapophyses. The facets meet medially, at which point there is a small vertical flange separating them. The internal surface of each wall of the arch bears a small median projection above the centrum. This projects either horizontally or dorsomedially. Postzygapophyseal facets are markedly elongate teardrops, which extend anteroposteriorly. The lateral edges are upturned.

Transverse processes are lacking, but a lateral flange is situated just posterior to each anterior cotyle.

SECOND CERVICAL (T1). The condyle is a laterally compressed oval in anterior view, with a low ridge about the circumference and the anterior end gently rounded, but terminally flattened. The posterior cotyle is a horizontally extended oval with the dorsal and ventral borders slightly flattened. The dorsal rim is anteriorly excavated. There is no infilling, but the chordal area is plugged by calcified tissue. Hypapophysis and basapophyses are absent.

The neural canal is large with a strongly arched roof. The roof can have a narrow, posteriorly extending excavation between the prezygapophyses, but its presence and development are variable. The foramina for the spinal nerves are large, piercing the arch wall just behind the transverse process on either side; in addition, small foramina are present anterior to the transverse processes. The neural crest is a low, narrow ridge extending the length of the arch. It rises to a high point in the centre of the roof and slopes posteriorly from there. A small ridge sometimes separates two posteroventral facets in this area. This ridge appears to be a function of age, large individuals possessing the structure. Prezygapophyseal facets are elongate teardrops, extending anteroposteriorly, and with the lateral edges slightly raised. Postzygapophyseal facets are long teardrops positioned anteroposteriorly and with the outer edges also raised. A small foramen pierces the arch just below the posterior edge of each prezygapophysis.

Transverse processes are short and robust. They are distinctly bicipital, widely separated, and the arms are joined by a web of bone. The dorsal arms originate from the middle of the arch, while the ventral arise from the anterior cotyle, just behind the point at which the condyle attaches. The arms are usually in the same vertical plane, although the ventral arms are occasionally anterior to the dorsal. Small posterior alar processes are present, pierced by a pair of small subcentral foramina.

TRUNK VERTEBRA (T7, see Fig. 21). The condyle is large, projecting almost to the front of the prezygapophyses. In anterior view the condyle is a dorsoventrally compressed oval. The front surface is flattened or slightly concave. There is a low, thick rim about the condyle anteriorly. The cotyle is a large oval with the dorsal border flattened. The lateral and, especially, the ventral rims form a cup for the condyle of the following vertebra. The cotyle is not infilled, but the chordal area is plugged, producing a flat anterointernal surface. Hypapophyseal structures and basapophyses are lacking.

The neural canal is small, triangular in anterior view, and the roof of the arch slants on either side of the median. Small foramina for the spinal nerves pierce the walls of the neural arch just behind the origin of each transverse process. A low triangular neural crest occupies the middle half of the roof. The roof rises above the postzygapophyses and bears ventrally a pair of indistinct facets separated by a low median ridge. The hyperapophyseal area ends posteriorly in a pair of gently convex edges. In large individuals a pair of projections may extend posteriorly, each one dorsomedial to one of the postzygapophyses. Prezygapophyseal facets are oval or teardrop-shaped, positioned anteroposteriorly, and the lateral edges extend dorsally. Postzygapophyseal facets mirror the prezygapophyses. A distinct lateral flange runs along the arch on either side, joining the zygapophyses to the transverse processes.

Transverse processes are short and distinctly bicipital. Dorsal and ventral arms originate midvertebrally, angle posterolaterally, and are weakly divergent with a web of bone between. Both arms are in a single vertical plane, the dorsal extending slightly beyond the ventral. Ventral arms are slightly greater in diameter than the dorsal. Small ventral struts brace the tranverse processes, one anterior and one posterior, with a large subcentral foramen on either side of the centrum. A small vertebrarterial foramen pierces the ventral arm of each transverse process next to the centrum.

SACRUM (T16). The anterior condyle is short and, in anterior view, a large dorsoventrally compressed oval. The anterior surface is slightly concave and is surrounded by a low rim. The posterior cotyle is a dorsoventrally compressed oval with a flat dorsal surface. The ventral rim extends slightly posteriorly. Infilling is absent, but a plug of calcified tissue fills the chordal area, forming a flat anterointernal surface. Hypocentral structures are lacking. A number of irregular subcentral foramina are present on either side of the centrum.

The neural canal is high, appearing triangular in anterior view. The foramina for the exit of the sacral nerves are large and located just behind the transverse processes, one on either side of the arch. The neural crest is a long, low triangle occupying the second quarter of the length of the arch. The arch rises posteriorly and bears a pair of indistinct facets ventrally between the postzygapophyses. Prezygapophyseal facets are elongate ovals, extending anteriorly and slightly laterally. The facets are slightly tilted from the horizontal and are situated well below the top of the neural arch. Postzygapophyseal facets are irregular ovals, extended anteroposteriorly, and with the lateral edges deflected dorsally.

Transverse processes are long and robust, originating midvertebrally, and forming acute angles with the centrum. The arms are robust and filled with calcified cartilage. Dorsal arms are of somewhat greater diameter than the ventral, but both are of the same length and are aligned in a single vertical plane. Small ventral lamellae are present on the ventral arms, and the tranverse processes are pierced by small vertebrarterial canals.

HAEMAL VERTEBRA (H3). A well-developed condyle projects a short distance past the centrum. It is a dorsoventrally flattened oval with a flat anterior surface and a low, distinct rim. The posterior cotyle is subcircular with a flattened dorsal rim and the ventral rim extending somewhat posteriorly. Infilling is absent, but the chordal area is plugged with calcified cartilage as in the trunk series. A large haemal canal is enclosed by a haemal arch arising from the posterior three quarters of the centrum. The arch extends posteroventrally and bears a small triangular crest and haemal aliform process.

The neural canal is high and narrow with the roof strongly arched above. A small foramen for the spinal nerve is present in the wall behind each transverse process. The neural crest extends the length of the arch, running straight forward from the rear of the arch, then sloping down to between the prezygapophyses. The hyperapophysis is present as a small, but distinct, aliform process above the postzygapophyses. The resulting facets face posteromedially. Prezygapophyseal facets are teardrop-shaped, positioned anteroposteriorly, and the lateral edges are raised. Postzygapophyseal facets are small, elongate teardrops extending anteroposteriorly in the horizontal plane.

Transverse processes are unicipital, in the form of thin vertical plates attaching to the neural arch and centrum and extending posterolaterally. Posterior alars form irregular ventral lamellae, pierced by numerous foramina. There is a small vertebrarterial canal on either side.

VARIATION ALONG THE COLUMN. *1. Condyles and cotyles.*- A short anterior condyle is formed along the column, but there is not a ball-and-socket joint as seen in procoelous lizards or frogs. Rather, the notochordal tissue remains in the joint, the condyle serving to strengthen and prevent disarticulation. The condyle is surrounded by a rim, which fits into the preceding cotyle. T1 has a small condyle compressed dorsoventrally and with a gently convex anterior surface. In the next few vertebrae the condyle is subcircular and the anterior surface gently concave. The rim is retained. After T4 or T5 the condyle is oval and the anterior surface remains concave. The remainder of the trunk vertebrae to the sacrum retain this form of condyle, with the most posterior trunk vertebrae and sacrum having the dorsal edge flattened. This structure obtains through the postsacral and into the haemal series, with the dorsal part of the condyle tending to be further anterior than is the ventral. In the more posterior haemals the condyle becomes circular. In smaller individuals the most posterior haemals are amphicoelous.

The posterior cotyle forms a cylinder to grip the rim of the anterior condyle and to enclose the notochordal tissue. The cotylar cup has smooth internal walls and an anterointernal flattened surface formed of the calcified tissue that is plugging the chordal area. The atlantal cotyle is weakly oval, the long axis dorsoventral. That of T2 is a large dorsoventrally flattened oval. Dorsal and ventral surfaces are slightly flattened and the rim is not posteriorly extended. Posteriorly along the column the dorsal surface of the cotyle is flattened, correlating with the structure of the corresponding condyle.

The dorsal rim of the cotyle is anteriorly excavated to a minor degree. This situation obtains throughout the remainder of the trunk vertebrae, the sacrum, and the postsacrals. The cotyle of the haemal vertebrae is circular, with the rim of equal extent on all edges.

2. *Hypapophyseal structures.*- Hypapophysis and basapophyses are lacking throughout the trunk. The haemal arch is present from the second or third postsacral on. In males the first haemal arch bears a posteroventrally projecting spine, whereas females tend to have the first haemal arch developed as a simple semicircle of bone attaching to the most posterior part of the centrum. There are, however, intermediates. The following haemals possess a crest, haemal process, and the arch extends anteriorly to arise along the ventrolateral edges of the centrum. The arch resembles the corresponding neural arch, except for the absence of zygapophyses and lesser extent posteriorly. A haemal arch is present until the last three or four caudal vertebrae, which are simple, amphicoelous spools.

3. *Neural arch.*- Spinal nerve foramina are present in all vertebrae. Small foramina pierce the atlantal neural arch posterodorsal to the anterior cotyles. The foramina are buttressed posteriorly by low, robust ridges. In T1 there are small anterior and larger posterior foramina. From here decrease in the size of the posterior foramina occurs until, in the last trunk vertebra and sacrum, they greatly enlarge for the nerves associated with the pelvic girdle and limbs. Only T1 has foramina anterior to the transverse processes. Small foramina are retained through the postsacral and haemal vertebrae.

The neural canal is large in the atlas and T1. There is then a steady decrease in size until the midtrunk region, where the canal increases, becoming maximum in the sacrum. The roof of the neural arch is swollen and extends anteriorly, almost covering the anterior condyle when the vertebrae are viewed dorsally. However, there is an open groove excavated in the anterior part of the roof between the prezygapophyses of the first few vertebrae of some specimens. T1 through T4 may have this excavation, only T1 may have it developed, or it may be lacking from the column. G,

4. *Neural crest and hyperapophysis*.- A low ridge often occupies the anterior half of the roof of the atlas, but this is dwarfed or obliterated by a large, thick boss covering the neural arch dorsally. The neural crest of T1 runs almost the length of the roof, but is low, the highest point being midway along the neural arch so as to form a low triangular spine in lateral view (contrast *T. vulgaris*). In T2 this crest is as in T1. Throughout the remainder of the column the crest is of less longitudinal extent, but of the same relative height as in T1 and T2. In the last trunk vertebra and in the sacrum the crest is a low triangle, occupying the second quarter of the roof of the neural arch. Postsacrally there is a marked increase in the height of the crest, which extends straight anteriorly from the top of the hyperapophysis, then slopes steeply to behind the front of the neural arch. The neural crest of the trunk region is similar to that in *Salamandra*, being markedly different from those in other species of *Triturus* and related newt genera.

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Aliform processes are lacking from the trunk vertebrae, sacrum, and postsacrals, but are present in the atlas and haemal vertebrae. In the trunk vertebrae the rear of the arch rises above the postzygapophyses and terminates in a pair of horizontally projecting posterior lobes as in *Salamandra*. The atlantal hyperapophysis is represented by a pair of deep facets rising dorsomedially from the postzygapophyses and separated by a vertical median ridge of bone. In the haemal series the aliform process forms a gently curving, V-shaped structure above the postzygapophyses. This encloses a posteriorly directed, shallow facet. This condition obtains until the most posterior caudals.

5. *Zygapophyses*.- Throughout the column prezygapophyses are closely appressed against the sides of the neural arch and project anterior of the end of the arch. Prezygapophyseal facets are irregularly teardrop-shaped, excepting in the haemal series where they tend to be oval. Facets are sharply tilted from the horizontal and extend anterolaterally.

Postzygapophyseal facets are variable and smaller than the corresponding prezygapophyses. Atlantal zygapophyses are narrow, elongate teardrops. Postzygapophyses of the trunk are variably teardrop-shaped, sometimes being approximately diamond-shaped. Facets extend anteroposteriorly and posterolaterally, and are inclined from the horizontal. Zygapophyses are present in all but the final six or seven caudal vertebrae.

6. *Transverse processes*.- Transverse processes are lacking from the atlas. Those on T1 are short, relatively robust, and deflected

posteriorly. Ventral arms originate just behind the anterior condyle and extend horizontally. The larger dorsal arms originate above the ventral and diverge dorsally. The arms are in a single vertical plane, connected by a web of bone, and with the dorsal arms extending slightly further posteriorly than the ventral. Both arms are filled almost to their distal ends by calcified tissue.

Posteriorly along the column, the following changes take place: transverse processes shift their origins posteriorly and attach midvertebrally; dorsal and ventral arms become thinner and (at about T3) the ventrals are of greater diameter than the dorsals; the arms become less divergent, until, in the most posterior part of the trunk, they parallel one another, although remaining bicipital; transverse processes of the immediately presacral vertebrae are thin, delicate structures.

Dorsal and ventral arms are in a common vertical plane throughout the column and small, but distinct, ventral lamellae are present on the ventral arms of all trunk vertebrae. In the more posterior trunk region a small ridge extends along the anterior face of each transverse process just below the dorsal arm. This ridge extends onto the neural arch and blends into the base of the prezygapophysis on either side. Except in the second cervical, ventral lamellae are pierced by large, irregular subcentral foramina. The vertebrarterial canals are small throughout the column. On T1 the ventral lamellae are robust plates of bone, imparting a triangular appearance to each transverse process in ventral view. Farther back, lamellae become progressively less robust. In the midtrunk region, and hence posteriorly, a pair of large subcentral foramina is present on each vertebra. These become so large as to all but obliterate the ventral lamellae, reducing the latter to anterior and posterior struts joining each ventral arm to the centrum.

Sacral transverse processes are large and strongly inclined posteriorly. The dorsal arms are of greater diameter than the ventral. One or two postsacral vertebrae are present, with long, thin transverse processes, in which the dorsal arms are absent and the ventrals do not bear ribs. The second or third vertebra behind the sacrum bears the first haemal arch; its transverse processes are long, thin, and unicipital. In the next five or six haemals, the transverse processes are thin, vertical flanges of bone projecting posterolaterally from the centrum. These flanges are reduced along the haemals to finally disappear, leaving the centrum with irregular networks of spongy bone laterally.

viii) Family Sirenidae Gray 1825

Siren Linnaeus 1766

Specimens.- One skeleton (UA 14404) of *Siren lacertina* and one cleared and stained (UA 14486) *Siren intermedia*.

ATLAS (see Fig. 11). Anterior cotyles are large, dorsoventrally compressed ovals, the lateral borders lower than the medial. Viewed laterally, there is a slight posterior tilt to the cotyles and they are very slightly concave. The odontoid process is a small, spike-like, dorsally situated process, which is an anterior continuation of the cotyles. The posterior cotyle is broadly teardrop-shaped with the lower border produced ventrally. There is a small amount of uniform infilling and the relatively large chordal foramen opens dorsally. Hypapophyseal structures are lacking, but laterally projecting flanges are present on each side of the centrum posteriorly.

The neural canal lies above the level of the anterior cotyles. The walls of the arch are thin, curving dorsomedially into the roof. A flange of bone is present on the inner side of each neural arch wall just dorsal to the centrum. The roof of the arch extends posteriorly to give rise to the postzygapophyses ventrolaterally. A pair of low, thin lateral flanges extends the length of the roof. The hyperapophysis is represented by a small aliform process, which is bisected posteromedially by a vertical flange of bone. Postzygapophyseal facets attach to the ventrolateral edges of the aliform process. They are small ovals having the lateral edges strongly inclined from the horizontal.

A short, relatively thick unicipital process arises from the posterodorsal part of each anterior cotyle and projects laterally and ventrally. The transverse process thus developed does not bear a rib.

SECOND CERVICAL (T1). The anterior cotyle is teardrop-shaped with the vertical axis greater than the horizontal. There is no infilling, the chordal foramen is far dorsal, and the ventral rim is produced anteriorly and ventrally. The posterior cotyle is subcircular, with no infilling, the chordal foramen is large and far dorsal, and the ventral border extends posteroventrally. A relatively low, but robust hypapophyseal keel is present. Basapophyses are lacking and there is a small subcentral foramen on one side or the other of the hypapophysis.

The neural canal is large and covered by an arched roof. I can distinguish no foramina for spinal nerves (but see Edwards 1976). The neural crest is low, does not rise above the aliform process, and extends over the anterior half of the roof of the arch. The aliform process consists of two arms, which extend anteromedially from above each postzygapophysis to the midpoint of the neural arch. The aliform process is somewhat lower than that of the posterior trunk vertebrae. Prezygapophyseal facets are subcircular and extend anteroposteriorly. They are steeply inclined dorsolaterally, such that the two facets face one another. Postzygapophyseal facets are irregular circles tilted from the horizontal.

Transverse processes originate midvertebrally from the centrum and neural arch and extend posteriorly at a steep angle. They are bicipital with nondiverging rib-bearers. Small first alar processes are present. Second alar processes extend from the ventrolateral borders of the anterior cotyle, posteriorly along the centrum and bases of the transverse processes. Third alar processes are low ridges running from the interzygapophyseal ridges along the anterodorsal surfaces of the transverse processes. Small vertebrarterial canals are present.

TRUNK VERTEBRA (T22, see Fig. 12). The anterior cotyle is large and circular, with no extensions from the rim. The posterior cotyle is subcircular- to teardrop-shaped, and the ventral half of the rim is produced posteroventrally. The chordal foramen is dorsal and infilling of the cotyles is lacking. A well-developed hypapophyseal keel extends from cotyle to cotyle. Basapophyses are absent, but two small subcentral foramina are present.

The neural canal is low, with the roof sloping steeply. Small spinal nerve foramina open beneath the interzygapophyseal ridges, just dorsal to the centrum on either side. The neural crest is thin and tall, rising well above the level of the aliform process. It extends approximately over the middle half of the arch. The top of the rear of the neural arch is flat and two vertical sheets of bone arise, one over each postzygapophysis, and extend anteromedially to unite with the neural crest. In dorsal view a V-shaped structure is, therefore, evident on the posterior third of the neural arch. Prezygapophyseal facets are of irregular shape, extending laterally and dorsally from the dorsolateral borders of the anterior cotyle. They are strongly tipped from the horizontal. Postzygapophyseal facets are subcircular, with the posterior and lateral borders raised. There is a well-developed interzygapophyseal ridge connecting the anterior and posterior zygapophyses on either side of the neural arch.

Transverse processes are long, thin unicipital rods arising from the midpoint of the centrum and extending ventrolaterally and somewhat posteriorly. Ribs are lacking. A complex system of alar processes is developed about each transverse process (see Fig. 1). Posteriorly a small flange joins the proximal part of each transverse process to the posterior cotyle (the first alar process). Anteriorly a large second alar process extends from the full length of the transverse process along the centrum and terminates bluntly beyond the anterior cotyle. The third alar process arises on the anterodorsal edge of the transverse process and extends to the centrum. The second and third processes form a deep cavity between them opening anterolaterally.

SACRUM. There is no sacral vertebra.

HAEMAL VERTEBRA (H5). The anterior cotyle is subcircular and the chordal foramen is set dorsally. The posterior cotyle is of similar shape, but with the foramen located further dorsally. Both cotyles lack infilling and there are no extensions of the rims. Strictly speaking, a haemal arch is not developed. A pair of hypapophyses arise from the entire length of the centrum ventrolaterally. These diverge slightly from each other terminally and the anterior edges are shorter than the posterior. A subcentral foramen is present beside each hypapophysis externally. These ventral processes are undoubtedly homologous to the lateral walls of the haemal arch in other urodeles, but a complete arch is lacking.

The neural canal is low, with the roof strongly arched. A small foramen pierces the wall of the neural arch on each side just posterior to the midpoint of the vertebra. The neural crest is a low, sharp spike occupying the middle third of the roof of the arch just anterior to the aliform process. A well-developed aliform process is present, but its floor is excavated anteriorly. The process extends posteriorly beyond the postzygapophyses. Facets of the zygapophyses are ovals extending anteroposteriorly and inclined dorsolaterally so as to be almost vertical. Faint interzygapophyseal flanges are present dorsolaterally on the arch.

Transverse processes extend laterally as obtuse triangles in the horizontal plane. The complex alar processes of the trunk region are lacking.

VARIATION ALONG THE COLUMN. *1. Cotyles*.- Except in the caudal vertebrae, anterior and posterior cotyles of the same vertebrae differ. Anterior cotyles are subcircular except for that of T1, which is a dorsoventrally compressed oval. The posterior cotyle differs in having a narrower ventral rim. This imparts a broad teardrop shape to the posterior cotyle. In the haemal series both cotyles are subcircular.

2. Hypapophyseal structures.- Excepting the atlas and cloacal vertebrae, a hypapophysis is present on all vertebrae. In the trunk series the hypapophysis bisects the basin formed by the ventrally deflected first and second alar processes. This subcentral keel is a thin median sheet of bone joining the anterior and posterior cotyles and not extending below the level of the cotyles. A pair of subcentral foramina are present, one on either side of the subcentral keel. In the cloacal region the subcentral keel is gradually reduced until, in about four cloacal vertebrae, it disappears. Posteriorly are two longitudinal ridges on the ventrolateral edges of the centrum. These paired hypapophyses become long, but never fuse distally into a haemal arch.

Basapophyses are absent, although it has been suggested (Estes 1964) that they are functionally replaced by basapophyseal-like processes of the second alar processes. This is discussed below (see description of the trunk musculature and Conclusions).

3. Neural crest and aliform process.- The atlas bears a pair of neural crests originating close together on the posterior border of the roof of the neural arch and diverging forward along the lateral borders of the arch. In T1 the neural crest remains below the level of the aliform process, but in all following vertebrae the crest is well above the aliform process. The neural crest is a thin, rectangular plate of bone. In the cloacal series the crest decreases in height, coming to be on a level with the aliform process. In the caudal vertebrae the crest drops below the aliform process, but remains distinct (although small) until the neural arch disappears in the ventrally deflected part of the tail.

In the large *Siren lacertina* an aliform process is present on the atlas, but this is lacking from the smaller *Siren intermedia*, in which the neural arch is flat posteriorly. The aliform process is present and well developed throughout the column, although the floor becomes reduced in the caudals. Only in the most posterior caudal vertebrae does the aliform process fail to develop.

4. *Zygapophyses*.- Zygapophyseal facets are similar throughout much of the column. Prezygapophyseal facets are oval and extend anterolaterally. Those of the postzygapophyses are variable, being either teardrop-shaped or subcircular. Both are tilted from the horizontal, particularly in the atlas and first three trunk vertebrae. Throughout the remainder of the trunk tilting is gentle, but it becomes pronounced in the caudal series. Anterior and posterior zygapophyses are joined by a ridge of bone extending along the lateral edge of the neural arch. This interzygapophyseal ridge is lacking from the atlas and from most of the caudals, but is present on all other vertebrae.

5. *Transverse processes*.- Except for the most posterior caudals, transverse processes are present throughout the column. In the atlas, the

transverse process is a small posterolaterally projecting spike originating from the base of the neural arch and posterodorsal surface of each anterior cotyle. The second cervical has nondiverging bicipital rib-bearers that carry robust, anteroposteriorly flattened ribs. The transverse processes project posterolaterally at an acute angle with the centrum, extending well behind the posterior cotyle. First, second, and third alar processes are present, but proportions and orientations differ from those of the more posterior trunk vertebrae. The second alar process projects almost straight ventrally and does not extend beyond the anterior cotyle. The third alar is a small ridge pointing dorsally with no anterodorsal component.

The transverse processes of T1 and T2 are similar, but those of the latter are more robust, with the dorsal and ventral arms divergent. The transverse processes are strongly angled posteriorly, but they do not project behind the posterior cotyle. Alar processes on T2 resemble those of T1, but the second alar processes have anterior basapophyseal-like projections, which do not extend in front of the anterior cotyle. T3 and T4 are generally as T1, with distinctly bicipital rib-bearers. However, the basapophyseal-like processes of the second alar processes project beyond the anterior cotyle.

Posteriorly the following trends are evident: the transverse processes become less posteriorly oriented and unicipital until, by T17 or T18, they end in a point; the second alars become less obliquely oriented, larger, and with broader basapophyseal-like processes; third alar processes come to be oriented anterodorsally and increase in relative size, capping a cavity with the second alar process below.

In the cloacal region the third alars become progressively reduced, finally disappearing in the first haemal vertebra. Second alars are also reduced, the basapophyseal-like projections disappearing in the beginning of the cloacal series. Finally, first and second alars become subequal and the transverse processes project at right angles from the centrum and are tipped ventrally. In the terminal caudal vertebrae, which are deflected ventrally from the remainder of the column, transverse processes are absent.

Chapter II

DESCRIPTIONS OF THE TRUNK MUSCULATURE

A. Introduction

Little work has been done on the deep structure of the trunk musculature and its relationships to the vertebrae, with most authors considering the *dorsalis trunci* and *subvertebralis* as uniform units throughout the Caudata. Maurer (1892, 1911) provides a major contribution to understanding the lateral abdominal musculature. He described the units of this portion in *Cryptobranchus*, *Amphiuma*, *Ambystoma* (neotenic and metamorphosed), *Necturus*, *Proteus*, *Salamandra*, *Triturus*, and *Siren*. My findings are in basic agreement with those of Maurer, with discrepancies in our observations having been noted in the descriptions. Auffenberg (1959, 1962) supplied the only dissection of the *dorsalis trunci* in salamanders. He (1959) described myoseptal patterns and basic tracts of muscle fibers in *Necturus*, *Siren*, and *Amphiuma*, providing a terminology for intermyoseptal, myoseptal-vertebral, and intervertebral fibral tracts. I have not found Auffenberg's terms to be useful descriptively or for comparison across familial lines, and do not follow them. Instead, I concentrate on the shape of the myomeres and their relationships to the vertebrae. My findings also differ substantially from Auffenberg's in certain areas, which are noted below.

Each species is considered separately according to the following format: The present range of the species and its habitat are given.

The fossil record, if any, of the genus and/or species is noted. A brief summary of what previous workers have suggested to be the relationship of the genus and/or species is provided. Remarks on the general body shape, length of the trunk, number of vertebrae in the trunk, and other factors are made. Next follows the description of the epaxial musculature (*dorsalis trunci*), hypaxial musculature (*subvertebralis*), and lateral abdominal musculature, in that order. Along with the description comparisons with other taxa are provided and, where necessary, comments made on the findings of previous investigators. It has proved necessary to name certain parts of the *dorsalis trunci* and *subvertebralis* for ease of referral. These names are not latinized and generally follow from some salient feature of the vertebrae with which they are associated.

Figures are provided for the majority of the described species. These consist of dorsal and ventral views of the musculature from the midtrunk region. In each figure the abdominal musculature has been cut midventrally and is spread laterally. The muscle units are drawn such that superficial layers have been removed in certain areas so as to expose underlying units. The muscle fibers are represented diagrammatically by straight lines extending between adjacent myosepta, which are drawn with heavier lines. Units located more superficially are represented by more widely separated lines, those located deep to these are shown with lines separated by a progressively narrower distance. For some species cross-sectional and lateral views are provided in order to show pertinent features. Muscle units are labelled appropriately.

Dissections were carried out by means of a dissecting binocular microscope, using fine tweezers and insect pins. Muscle fibers were gently pulled and teased away so as to show the shapes of the myomeres of the *dorsalis trunci*, the septal patterns within the *subvertebralis*, and to expose underlying muscle units. In preparing the figures, dorsal and ventral drawings of cleared and stained specimens were made using a camera lucida. These drawings then served as the basis on which to sketch the units of the trunk musculature. In the figures the numbers of the first figured trunk vertebrae are given, as well as the scale in millimeters. Unless otherwise noted, specimens are metamorphosed adults.

Representatives of the following species were studied (number skeletonized, number cleared and stained, number of alcoholic specimens, except as noted all specimens catalogued in the Department of Geology, The University of Alberta):

Hynobiidae
- *Hynobius retardatus* (0, 1, 4)
- *Hynobius naevius* (1, 1, 3)
- *Pachypalaminus boulengeri* (1, 1, 2)
- *Onychodactylus japonicus* (4, 5, 8)

Cryptobranchidae
- *Cryptobranchus alleganiensis* (1, 2, 3)

Amphiumidae
- *Amphiuma tridactylium* (1, 0, 3)
- *Amphiuma pholeter* (0, 0, 1)

Ambystomatidae

Dicamptodon ensatus (0, 2, 5)

Rhyacotriton olympicus (0, 1, 3)

Ambystoma macrodactylum (0, 2, 2, UA-MZ)

Ambystoma gracile (1, 1, 4)

Ambystoma maculatum (2, 2, 2)

Ambystoma jeffersonianum (2, 1, 2)

Ambystoma opacum (1, 1, 5)

Ambystoma talpoideum (1, 1, 3)

Ambystoma cingulatum (0, 1, 3)

Ambystoma tigrinum (15, 7, 22)

Proteidae

Necturus maculosus (3, 1, 4)

Proteus anguinus (0, 0, 2, UW-RCS)

Plethodontidae

Plethodon jordani (3, 1, 4)

Plethodon glutinosus (0, 1, 3)

Plethodon cinereus (0, 1, 2, UA-MZ)

Plethodon vehiculum (0, 1, 3, UA-MZ)

Plethodon neomexicanus (0, 1, 2, UA-MZ)

Ensatina eschscholtzii (0, 2, 4, part UC-MVZ)

Aneides lugubris (2, 3, 9, part UC-MVZ)

Aneides aeneus (0, 0, 2, UA-MZ)

Aneides ferreus (0, 0, 2, UA-MZ)

Hemidactylium scutatum (0, 1, 3)

Batrachoseps attenuatus (0, 1, 4)

Bolitoglossa subpalmata (0, 1, 2, UC-MVZ)

Pseudoeurycea cephalica (0, 1, 5, UA-MZ)

Chiropterotriton chiroptera (0, 1, 3, UA-MZ)

Chiropterotriton chondrostega (0, 0, 4, UA-MZ)

Chiropterotriton xolocalcae (0, 0, 2, UA-MZ)

Hydromantes brunus (0, 0, 1, UC-MVZ)

Eurycea bislineata (0, 1, 2)

Eurycea quadradigitata (0, 2, 4)

Eurycea junaluska (0, 0, 2)

Typhlotriton spelaeus (0, 1, 2, AMNH)

Gyrinophilus porphyriticus (1, 2, 4)

Pseudotriton ruber (1, 1, 5)

Stereochilus marginatus (0, 1, 2, AMNH)

Desmognathus fuscus (4, 2, 4)

Desmognathus monticola (0, 1, 0)

Desmognathus orchrophaeus (0, 1, 5)

Leurognathus marmoratus (0, 1, 2, AMNH)

Salamandridae

Salamandra salamandra (1, 2, 2)

Salamandra atra (1, 0, 3)

Pleurodeles waltli (1, 1, 2)

Tylototriton andersoni (0, 0, 1)

Salamandrina terdigitata (0, 1, 2, AMNH)

Notophthalmus viridescens (4, 7, 15)

Notophthalmus perstriatus (0, 0, 4)

Taricha (*T. torosa* and *T. granulosa*) (6, 2, 5)

Cynops pyrrhogaster (3, 2, 3)
Cynops ensicauda (0, 1, 0)
Paramesotriton hongkongense (2, 2, 11)
Triturus cristatus (11, 5, 12)
Triturus marmoratus (2, 1, 3)
Triturus alpestris (1, 1, 2)
Triturus vittatus (0, 1, 4)
Triturus vulgaris (6, 7, 5)
Triturus helveticus (0, 1, 2)
Euproctus asper (1, 1, 2)

Sirenidae

Siren intermedia (0, 1, 3)
Siren lacertina (1, 0, 1)

B. Descriptions

i) Family Hynobiidae Cope 1859

Hynobius Tschudi 1839

RANGE. Found in Korea, the Japanese islands, eastern China, and throughout most of eastern Russia (Thorn 1968).

HABITAT. Larvae are of the pond type, being found in still ponds and small lakes. Metamorphosis into a terrestrial adult is almost invariable, but neoteny is known (Thorn 1968, Sasaki 1924).

FOSSIL RECORD. None known.

RELATIONSHIPS. Regrettably little work has been done on the systematics of this genus, with Dunn's (1923a) monograph remaining the only coverage. *Hynobius* is generally considered the most primitive living hynobiid (see Dunn 1923a, Noble 1931). Dunn (1923a) divided *Hynobius* into four species groups, a separation followed by Thorn (1968), but with the addition of subsequently named species and nomenclatorial corrections. These groups are as follows:

1. Mainland group, considered to be the most primitive: *H. keyserlingii*, *H. leechii*, *H. chinensis*, and *H. shihi*. *H. leechii* was suggested as an acceptable "ancestor" for the following two groups.

2. *H. nebulosus* group: *H. nebulosus*, *H. tsuensis*, *H. dunni*, and *H. abei*. These species have a laterally compressed tail, tend to breed in standing water, and are found in the southern parts of Japan (Thorn 1968).

3. *H. lichenatus* group: *H. lichenatus*, *H. nigrescens*, *H. sadoensis*, and *H. retardatus*. This is Dunn's (1923a) *H. peropus* group, with this species having been subsequently split into *H. lichenatus* and *H. nigrescens*. The group is found in the northern parts of Japan, tends to have laterally compressed tails, and breeds in streams, ponds, and lakes (Thorn 1968). *H. retardus* was available for study.

4. *H. naevius* group: *H. naevius*, *H. kimurai*, *H. okiensis*, *H. stejnegeri*, and *H. sanani*. This group tends to have relatively short, thick tails and breeds in streams with rocky bottoms (Thorn 1968). *H. naevius* was available for study.

Of these groups, only representatives of the supposedly more derived island groups have been examined. *H. naevius* and *H. retardatus* are similar in the structure of their trunk musculature, in spite of ecological differences. Owing to the relatively small sample from *Hynobius*, intrageneric variation is unknown and conclusions are tentative.

Hynobius retardatus Dunn 1923

RANGE. Restricted to the island of Hokkaido, Japan (Thorn 1968).

HABITAT. Lakes, ponds, stagnant water, and the surrounding land (Thorn 1968).

FOSSIL RECORD. None known.

RELATIONSHIPS. Placed in the *H. lichenatus* species group (Thorn 1968), which apparently represents a relatively derived lineage of independent derivation from the mainland species (Dunn 1923a).

REMARKS. The trunk is relatively short and robust, similar to that of the *Ambystoma tigrinum* group of ambystomatids (q.v.). There are twelve, sometimes eleven, costal grooves between the limb girdles (Dunn 1923a). These reflect the number of myomeres spanning the same distance. As in other amphicoelous salamanders, a significant part of the epaxial myomere is distal to the vertebral column, forming intermyoseptal muscle masses.

Epaxial musculature (see Fig. 22).- The myoseptum attaches along the dorsal surface of the rib, extends along the posterodorsal surface of the transverse process, and then along the lateral edge of the posterior zygapophysis to the neural process. In the posterior one-quarter of the trunk an extension of each myomere (posterior septum of the myomere) joins to the lateral surface of the neural process of the next posterior vertebra. This septal attachment is lacking in the anterior segments of the trunk musculature. It may function in providing additional, more direct pull by the myomere on the vertebra in the area from which most of the push for terrestrial locomotion originates.

Each myomere has a single, large anterior flexure next to the midline. These flexures partially overlap along the column, each resting over the posterior one third of its anterior neighbour. Thus, although a myomere only contracts directly between two vertebrae, anterior and posterior overlap causes each segment to influence three vertebrae. In dorsal view the full extent of the anterior flexure is not evident, but a deeper medial part is seen when the myomeres are pulled laterally. In each flexure the muscle fibers are oriented so as to produce a fan-shaped muscle. Distal to this, in the main mass of the myomere, the superficial layers are aligned anterolaterally. Moving ventrally and laterally along the surface of the myomere, however, the fibers gradually change orientation so that at the horizontal septum they extend anteroposteriorly. Beneath this thin dorsal layer the strands extend anteroposteriorly, paralleling the vertebral column. Rising from between the ribs and transverse processes of adjacent vertebrae, the main body of each myomere extends dorsally and posteromedially to overlap the next posterior myomere.

Hypaxial musculature (see Fig. 22).- The *subvertebralis* is complex and relatively thick. In ventral view only a small area at each intercentral joint is visible, the remainder of the vertebrae being covered by musculature. Each myomere spans two intervertebral joints, affecting three vertebrae during contraction. The myomeres are extensively folded so as to partially overlap (anteriorly) and underlie (posteriorly) their neighbours. The folding of the subvertebral complex is equalled only in other hynobiids, cryptobranchids, ambystomatids, and amphiumids.

The anterolateral surface of each centrum provides attachment for the medial section of the myomere. A septum extends anteriorly parallel to the next anterior centrum and posteriorly it proceeds back and slightly lateral. At the level of the transverse process of the next posterior vertebra, the myoseptum reverses to extend anteriorly to the distal edge of the ventral rib-bearers of the first vertebra. From here it runs along the ventral surface of the rib into the lateral abdominal musculature. The part of the septum extending anteriorly from each cotyle may be called the basapophyseal septum. Although in *H. retardatus* anterior basapophyses are present only as small thickened areas, the septum and its associated muscle is homologous to the anterior basapophyseal muscle of other hynobiids, cryptobranchids, ambystomatids, and amphiumids (see Conclusions).

The basapophyseal muscle is composed of fibers with two sorts of attachment. That is, the medial group extends anteromedially between the basapophyseal septum and the centrum. The lateral group bridges the basapophyseal septum and the septum of the next anterior myomere. The pinnate muscle thus formed has its origin on the lateral surface of the centrum and on the septum lateral to it (see Fig. 22). The insertion is on the lateral surface of the anterior cotyle in the anterior basapophyseal area (see descriptions of the vertebral column above). Such a pinnate muscle "can develop great force for its overall width, but has a short contraction distance" (Hildebrand 1974, p. 462). This part of the myomere will be termed the anterior basapophyseal muscle in all taxa in which a muscle with similar relationships is developed.

The most superficial ventral layer of the myomere partially underlaps and obscures the more medial fibers. Medially, these ventral fibers are fan-like, but they become anterolaterally extended towards the lateral abdominal musculature. At the lateral edge this sheet partially blends into the *transversus*. Beneath the ventral layer the form of the myosepta and their associated muscle fibers become clear. The posteriorly pointed, V-shaped flexure from the transverse process sends fibers posteromedially and posterolaterally into the next posterior, serially homologous septum. Both lateral and ventral to this transverse process flexure the intercostal group and the fibers between the rib-bearers are aligned parallel to the vertebral column. Upon contraction, however, the intercostal fibers shift from an anteroposterior orientation.

Except for the atlas, spinal nerves exit intervertebrally and extend posterolaterally through the myomere to the proximal tip of the ribs. Here each nerve is exposed to the peritoneal cavity for a short distance. It extends laterally and slightly anteriorly until the *transversus* is reached. From this point it proceeds laterally, parallel and just posterior to the myoseptum, between the *transversus* and *obliquus externus* to the *rectus abdominus*.

Lateral abdominal musculature (see Figs. 22 and 26).- The most external *obliquus externus* is relatively thick and divided transversely by myocommata. Its fibers extend posteroventrally, spanning the area between the *dorsalis trunci* and the *rectus abdominis*, partially overlapping each of the latter. Internally, next to the *o. externus*, is a very thick *transversus*, which extends anteroventrally. Medially the *transversus* blends with the intercostal musculature, ventrally it partially overlaps the *rectus abdominis* internally. *H. retardatus* possesses only these two units in the lateral body wall. Both the *obliquus externus profundus* and the *obliquus internus* are lacking. I consider this a primitive adult condition, with the addition of other layers being a foetal specialization (see Conclusions).

The *rectus abdominis* is divided into two parts: a ventromedial *rectus abdominis superficialis* and, dorsolateral to this, the *r. a. profundus*. The *r. a. superficialis* is divided by septa that are extensions from the *o. externus*. The septa of the *r. a. profundus* are, however, separated from those of the other abdominal groups, and extend anterolaterally rather than laterally and ventrally. The muscle fibers between these septa extend anterolaterally, and the *r. a. profundus* serves as a retractor of the tongue, linking the hyobranchium to the pelvic girdle.

Hynobius naevius (Temminck and Schlegel 1838)

RANGE. Restricted to Japan on the north and south parts of the island of Kyushu, northeastern Shikoku, and eastern Honshu (Thorn 1968).

HABITAT. Dunn (1923, pp. 483-484) quotes Tago (1907) on the areas inhabited by this species. Found in valleys having ponds and streams, "surrounded by hills and cliffs with cedar, elm, or chestnut . . . among moss, dead leaves around swamps, in bushes, under roots, rocks, or in deserted nests of water rats or moles. In short they like damp, shady places . . . free from sunshine." After rains the terrestrial adult comes to the surface and feeds on "worms, insects, and tiny fishes." Hibernation occurs on land, with breeding in the spring in water. Larvae are of the pond type.

FOSSIL RECORD. None known.

RELATIONSHIPS. This species is the type of the *H. naevius* species group (Dunn 1923a, Thorn 1968). The group is composed of species with short, thick tails, often breeding in streams with rocky bottoms (Thorn 1968). According to Dunn (1923a), *H. naevius* is closely related to only *H. kimurai* and *H. stejnergeri*, being relatively isolated.

REMARKS. The body is elongate but stout, with a short, rounded tail. There are usually 14 costal grooves. A somewhat lesser amount of musculature seems to be located dorsal to the vertebral column than in *H. retardatus*. In spite of the apparently differing niches of the two species, the trunk musculature of *H. naevius* is very like that of *H. retardatus*.

Epaxial musculature (see Fig. 23).- The myomeres of the *dorsalis trunci* are fundamentally as in *H. retardatus*. However, the anterior flexures are somewhat shorter and more acutely V-shaped. In dorsal view, the full development of the anterior flexure is evident only when the myomere is displaced laterally. The attachment of the myoseptum to the vertebrae and ribs is as in *H. retardatus*, but accessory attachments of the myomeres to posterior vertebrae appear to be lacking throughout the column.

The muscle fibers within the anterior flexures are situated as in *H. retardatus*. The fibers in the main body of each myomere, lateral to the anterior flexure, extend anteriorly and slightly laterally. Beneath this superficial layer the fibers orient anteroposteriorly. The main body of the myomere rises posterodorsally from between adjacent ribs.

Hypaxial musculature (see Fig. 23).- The pattern of the *subvertebralis* is also very similar to that of *H. retardatus*. This unit is thick, covering all of the ventral part of the column except for a diamond-shaped area below each intercentral joint. Distinct anterior basapophyseal muscles are present, attaching to low anterior basapophyses, which are developed even in small adults. Behind this pinnate muscle is the posteriorly directed, acutely V-shaped part of the myomere associated with the transverse process. This flexure is relatively somewhat longer than in *H. retardatus*.

The myoseptum extends straight along the rib, but near the union of the myomere with the *transversus* the septum inclines anteriorly such that each myomere slightly underlaps its anterior neighbour. In this it differs from *H. retardatus*. Also unlike the latter, the pattern of hypaxial myomeres is clear without removal of a superficial layer of muscle fibers. In the lateral part of the myomere superficial fibers extend anteroposteriorly and do not blend laterally with the *transversus*, except for a small band running anterolaterally from the anterolateral edge of each myoseptum. This band partially overlaps and blends with the *transversus*.

Proximal to the column, spinal nerves are as in *H. retardatus*. However, in the lateral body wall each nerve is directly adjacent to a myoseptum posteriorly. From here the nerves extend into the *rectus abdominus*.

Lateral abdominal musculature (see Figs. 23 and 26).- The *obliquus externus* is somewhat thinner than in *H. retardatus*; however, its topographic relationships to the other muscle segments and its orientation are the same. Also, as in *H. retardatus*, the *obliquus internus* is lacking in the adult.

The *transversus* is relatively thin and joins with the subvertebral myomeres in a manner differing from that in *H. retardatus*. In *H. naevius*, the *transversus* partially overlaps the epaxial myomeres and only blends with the intercostal muscles to a limited extent posteriorly. From here it extends laterally and slightly anteriorly, underlapping the *r. a. profundus* and attaching to the *r. a. superficialis* internally. The structure of the two part *rectus abdominis* is as in *H. retardatus*.

Pachypalaminus boulengeri Thompson 1912

RANGE. Limited to isolated populations in Japan: the Odaigahara plateau on Onshu, Mount Ishizuchi on Shikoku, and Mount Sobo on Kyushu (Thorn 1968).

HABITAT. Riparian in wooded and mountainous areas (Thorn 1968).

FOSSIL RECORD. None known.

RELATIONSHIPS. This monotypic genus is sometimes included in the genus *Hynobius*, from which it differs in having the lacrimal divided into two, cornified skin on the soles of the feet and tips of the toes, and a large premaxillary fontanelle (Dunn 1923a, Thorn 1968). Dunn (1923a, p. 505) considered it closest to *H. vandenburghi* (= *H. nebulosus*), of which it is possibly "a very local modification." The trunk musculature differs somewhat from that of the two species of *Hynobius* described above, but until intrageneric variation is elucidated in the latter generic separation is problematical.

REMARKS. The trunk is long, but very stout. There are generally 13 costal grooves. Based on the structure of the myomeres alone, generic recognition is perhaps justified.

Epaxial musculature (see Fig. 24).- The myomeres of the *dorsalis trunci* are developed as in *H. retardatus* and *H. naevius*, with minor modifications. The anterior flexures are short, as in *H. retardatus*, and obtuse. The inner part of each flexure is exposed dorsally without lateral displacement of the myomere. The single septum extending forward from the anterior flexure is relatively longer than in either species of *Hynobius* here described, extending to almost the posterior edge of the next anterior vertebra.

In the midtrunk region a septum extends back posteromedially from the main body of each myomere to insert on the anterior surface of the transverse process of the next posterior vertebra. This septum is present throughout the remainder of the myomeres posteriorly. The structure of the main body of the myomere is as in *Hynobius*.

Hypaxial musculature (see Fig. 24).- The complex folding within the *subvertebralis* is covered ventrally by a thin superficial layer of muscle fiber. Upon removal of this the pattern becomes clear. Well-developed anterior basapophyseal muscles are present. The posterior flexure from the transverse process is relatively narrower than in the other available hynobiids, owing to the fact that the myoseptum does not extend posteromedially from the joint between the rib and transverse process. Instead the septum runs along the transverse process to the latter's midpoint and then extends posteromedially into the muscle fibers of the next posterior myomere. *Pachypalaminus* is also unique in having a small, short septum extending forward at this point of reversal (labelled anterior flexure in Fig. 24).

In the main mass of each myomere lateral to the anterior basapophyseal muscle and transverse process flexure the muscle fibers proceed in several different, layered directions. Most ventrally they extend anterolaterally. Above this thin layer is a scattering of fibers running anterolaterally at a more obtuse angle. Above these, there is a layer of anteromedial fibers, followed dorsally by a unit extending anterolaterally. The myomere ventral to the ribs slopes slightly posteriorly.

Except for the atlas, spinal nerves exit intervertebrally. They are buried by the fibers of the *subvertebralis* proximally and are exposed to the peritoneum at the level of the bifurcation of the rib-heads. Each nerve remains on the ventral surface for some distance, passing along the *subvertebralis* to disappear external to the *transversus* at a notch formed between that muscle unit and the myoseptum (see Fig. 24).

Lateral abdominal musculature (see Fig. 24).- The lateral abdominal musculature is conformable to that in *Hynobius*. The *obliquus externus*, *rectus abdominis profundus*, and *r. a. superficialis* are as in the species of *Hynobius* described previously. The *transversus* differs in underlapping the posterodistal part of each subvertebral myomere and extending anterolaterally so as to expose part of the *o. externus* to the peritoneum. The *transversus* underlaps the *rectus abdominis* as in *Hynobius*. A further distinction is that part of the intercostal group extends beyond the tips of the ribs, between the *transversus* and the *obliquus externus*. It is possible that this extension from the intercostal group is homologous to the *obliquus internus* of other salamanders.

Onychodactylus japonicus (Houttuyn 1782)

RANGE. Found in the northern two thirds of the island of Honshu, Japan, except along the western coast (Thorn 1968).

HABITAT. Adults are found beside streams and ponds in wooded, mountainous areas. They are secretive under rocks, decaying logs and moss, preferring humid, cool, shaded areas. Breeds in rapid mountain streams (Thorn 1968).

FOSSIL RECORD. None known.

RELATIONSHIPS. Dunn (1923a) noted the basic similarity of this genus to *Hynobius*, considering the latter to be ancestral to *Onychodactylus*.

As regards the structure of the trunk musculature, *Onychodactylus* is readily derivable from *Hynobius* by means of paedomorphosis.

REMARKS. The trunk is long and relatively thin, with 13 or 14 costal grooves. A significant part of each myomere is located distal to the vertebral column. The tail is long, oval in cross-section, and well-muscled. "Claws" of cornified skin are present in larvae and breeding adults. The hind limbs are robust and the feet broadened.

Epaxial musculature (see Fig. 25).- The myosepta join with the vertebrae as in *Hynobius*. In the rear portion of the trunk a posterior septum from each myomere extends to the distal end of the transverse process and to the proximal end of the rib of the next posterior vertebra. Anterior flexures are very acute and relatively about twice as long as those in *Hynobius*. Each completely overlaps the next anterior vertebra and part of the second anterior. Thus the elongation causes the flexure to affect an additional vertebra in comparison to other hynobiids. This is presumably an adaptation to increase flexion of the trunk (compare *Amphiuma*) without adding vertebrae to the column. This modification is perhaps correlated with the mountain stream habitat of *Onychodactylus*. The main body of each myomere is inclined back as in *Hynobius*, and the direction of muscle fibers is comparable in the two genera. Hyperapophyseal muscles arise from the rear of the neural arches between the postzygapophyses. These are not pinnate.

Hypaxial musculature (see Fig. 25).- This species resembles *H. retardatus* in having a superficial ventral layer of muscle fibers obscuring the myoseptal pattern, and *H. naevius* in having the lateral part of the myomere slanted anteriorly. The thick *subvertebralis* completely covers the vertebrae except for small intercentral areas. Anterior basapophyses are especially prominent just posterior to the atlas. They decrease from here posteriorly, but remain present throughout the trunk even on relatively small individuals (see Fig. 2). However, the associated basapophyseal muscles, although well-developed, are not notably larger than those of other hynobiids.

The spinal nerve exits intervertebrally, passing through the *subvertebralis* dorsal to the posterior flexure from the transverse process. Each nerve is exposed peritoneally for a short distance intercostally and then disappears external to the *transversus*. The nerve passes between the *obliquus externus superficialis* and the *o. e. profundus* immediately adjacent to the posterior border of a myoseptum to disappear ventrally into the *rectus abdominis*.

Lateral abdominal musculature (see Figs. 25 and 26).- Unlike *Hynobius* and *Pachypalaminus*, *Onychodactylus* has four divisions of the lateral body wall. Dunn (1923a) and Noble (1931) argued that *Onychodactylus* arose from within the genus *Hynobius*, and the condition in the former is probably a paedomorphic derivation. Although larval hynobiids have not been available for this study, consideration of the Ambystomatidae (q.v.) make this likely. Larval ambystomatines of more primitive aspect have four layers, but these are usually lost in the adult.

The *obliquus externus superficialis* is conformable to the single *obliquus externus* of *Hynobius*. It is a thin layer, with fibers extending posteroventrally. Beneath this layer is the *o. e. profundus*, which is lacking in *Hynobius*. This layer is confluent with the intercostal fibers proximally and with the *rectus abdominis* distally. Its muscle fibers extend posteroventrally, but at a lesser angle than those of the *o. e. superficialis*. The anteroventrally aligned *obliquus internus* is deep to the inner part of the external oblique. It merges with the *rectus abdominis* distally, but does not join with the *intercostalis* proximally.

The most internal layer of the lateral abdominal musculature, the *transversus*, has fibers extending anteroventrally between myosepta at an angle greater than those of the *o. internus*. The *transversus* is segmented by myocommata only in its proximal one third. It merges with the *subvertebralis* dorsally and overlaps the *rectus abdominis* ventrally. Owing to the fact that the *o. internus* and *o. e. profundus* blend with the *rectus abdominis*, the latter is not a distinct unit. However, its boundaries may be taken as including that area in which the ventral muscle fibers extend anteroposteriorly. There is no sign of division into two parts.

Although *Onychodactylus* has four distinct layers of lateral abdominal musculature, the abdominal wall is notably thinner than that of the species of *Hynobius* here dissected.

ii) Family Cryptobranchidae Cope 1889

Cryptobranchus alleganiensis (Daudin 1803)

RANGE. "From southern and western New York [state] southward to northern Georgia, Alabama, Mississippi and westward to central Missouri" (Nickerson and Mays 1972, p. 3).

HABITAT. Completely aquatic in running water. Nocturnal, hiding under rocks and submerged logs by day (see Bishop 1943, Nickerson and Mays 1973).

FOSSIL RECORD. *C. alleganiensis* is known from the Pleistocene of eastern North America (Nickerson and Mays 1973). Other fossil cryptobranchids and the living Asian species are usually referred to the genus *Andrias*. I do not, however, recognize the validity of this taxon, considering it to be a junior synonym of *Cryptobranchus* (Naylor 1978c). *C. scheuchzeri* is known from the Oligocene to Pliocene of Europe, *C. matthewi* from the Miocene and Pliocene of North America, and *C. japonicus* from the late Pleistocene of Japan (Cook 1917, Thenius 1954, Westphal 1958, 1967, 1970, Shikama and Hasegawa 1962, Meszoely 1966). In addition, an extinct genus *Piceoerpeton* is known from the Paleocene and Eocene of central North America (Meszoely 1967, Estes 1969a), which may be a cryptobranchid.

RELATIONSHIPS. During the 1800's *Cryptobranchus* was often classified with *Amphiuma* in the family Amphiumidae (e.g., Gray 1825, Bonapart 1831, Boulenger 1882, 1910). Cope (1867, 1889), however, recognized the distinctions between the two taxa, placing them in separate families. The close relationship between cryptobranchids and hynobiids has long been accepted (Dunn 1922, Noble 1931). The two families share many features, most of them to be judged as primitive. I consider *C. alleganiensis* to be a relatively recent derivative from "*Andrias*", owing its distinctive characters to paedomorphosis (e.g., gill slits retained in adult, structure of the hyobranchium, see also below).

REMARKS. The trunk is long, very thick, and dorsoventrally compressed and laterally expanded. There are generally 13 myomeres between the limb girdles, but owing to folding of the skin costal grooves are not evident. The myomeres are relatively wide and the trunk is very flexible. A large mass of musculature is developed dorsolateral and lateral to the vertebral column.

Epaxial musculature (see Fig. 27).- The major departure of this species from the condition described for the Hynobiidae is in marked increase in the mass of epaxial musculature. A pair of distinct septa separates the left and right myomeres medially. Each myoseptum attaches to its medial septum above the neural process (hyperapophysis) of a vertebra. It then extends from the neural process down the posterior and lateral edges of the postzygapophysis to the proximal part of the transverse process. The myoseptum attaches to the postero-dorsal edge of the transverse process, along the rib, and then proceeds distally where it is unsupported by bone. The myomere extends much further laterally beyond the rib than is the case in hynobiids.

The myomere is complexly folded dorsal to its attachment to the vertebrae. Each anterior flexure extends anteriorly over about three quarters of the first vertebra of the pair spanned by its myomere. Thus it is relatively shorter than in hynobiids. The full extent of the anterior flexure is apparent only when the myomere has been displaced laterally. The flexures overlap about one half of the length of their anterior serial homologues. A long, deep septum proceeds forward from the apex of each V-shaped flexure into the muscle of the preceding flexure.

Laterally, the main body of each myomere slopes anteroventrally down to join the ribs of adjacent vertebrae. Dissection of contorted specimens shows that upon contraction of muscle fibers the septa of this part of the myomere come to be oriented almost vertically. The posterior septum from the myomere to the next posterior vertebra, seen in certain hynobiids, is apparently lacking throughout the column in *Cryptobranchus*.

Hypaxial musculature (see Fig. 27).- The very thick *subvertebralis* is folded as in hynobiids. Only a small, diamond-shaped area beneath each intercentral articulation is not covered by muscle fibers. Tough fascia encloses the hypaxial musculature ventrally. This fascia is continuous with the myosepta above. In superficial ventral view part of the more medial folding of the myomere is obscured by a thin layer of longitudinal muscle fibers. At their forward edges these overlap the posterior flexure from the transverse process. Upon removal of this sheet, the pattern is clearer, although spread of the myosepta onto the ventral surface confuses the pattern. In spite of such complexities, the basic design is hynobiid-like. Large anterior basapophyseal muscles are present, but anterior basapophyses are not present on the vertebrae. A long, wide transverse process flexure extends posteriorly just lateral to each basapophyseal muscle. From these posterior flexures long, deep septa extend posteriorly.

The short anterior flexure in the main body of each myomere is developed to a greater degree than in the Hynobiidae. The subcostal portion of the myomere slants posterodorsally between adjacent ribs. From the anterior edge of the anterior flexure a short septum extends forward parallel to the transverse process flexure of the next anterior myomere. A tough sheet of fascia runs between the anterior flexure and the baspophyseal muscle of the same myoseptum. This sheet is continuous with the myosepta dorsal to it and is also present in certain hynobiids. It underlies the transverse process flexure and, ventrally, provides attachment for the most superficial layer of the *subvertebralis*.

Spinal nerves are not exposed to the peritoneal cavity, perhaps owing to the thickness of the *subvertebralis*. Except for those associated with the atlas, they exit intervertebrally to pass through the intercostal muscles. Distally each is found between the *transversus* and *obliquus internus* just posterior to the myocomma of each segment.

Lateral abdominal musculature (see Figs. 27 and 47).- The musculature surrounding the viscera is thick laterally and thin ventrally. The *obliquus externus* does not overlap the epaxial musculature. Its fibers extend posteroventrally from the horizontal septum and are divided transversely by myosepta into parallel bands. A very thick *obliquus internus* is beneath the relatively thin *o. externus*. This deeper unit is a continuation without break of the intercostal muscles. Ventrally it is completely intergraded with the simple *rectus abdominis*. Although the muscle fibers of the *o. internus* are not oriented obliquely, it is here termed *obliquus internus* owing to positional relationships. However, it may be composed of both the *o. internus* and the *o. externus profundus*. Ontogenetic studies are necessary to resolve this.

The thin internal *transversus* intergrades proximally with the *subvertebralis*. Unlike the condition in hynobiids, the *transversus* is completely segmented, from proximal to distal edge, by myocommata. It extends almost at right angles from the *subvertebralis*, the fibers aligning only slightly anteroventrally. The *rectus abdominis* is not clearly differentiated, but can be considered the most ventral part of the *o. internus*, beyond the bounds of the *o. externus* and *transversus*. The *rectus abdominis* is very thin, with fibers extending anteroposteriorly between myocommata. Its thinness and simplicity are probably owing to support given the viscera by the surrounding water.

iii) Family Amphiumidae Gray 1825

Amphiuma tridactylium Cuvier 1827

RANGE. Southern part of the Mississippi River drainage basin: "Along the Gulf Coastal Plain from the Brazos River valley in Texas through the Mississippi alluvial plain to where this meets the eastern Gulf Coastal Plain . . . eastward into the western half of Alabama, and . . . north up the Mississippi valley as far as . . . Kentucky and . . . Missouri, up the Arkansas River valley . . . beyond Little Rock Arkansas, and up the Red River valley . . . [to] the southeastern corner of Oklahoma" (Salthe 1973b, p. 149.1). If, as seems likely, this is actually a subspecies of *Amphiuma means* Garder 1821, the species range extends eastward to the Atlantic Ocean, including Florida.

HABITAT. Found in "lakes, open-spring streams . . . and streams flowing over calcareous rocks. They are also reported in drainage ditches, bayous, and wooded alluvial swamplands" (Bishop 1943, p. 54).

FOSSIL RECORD. *Amphiuma means* is known from the Pleistocene of Florida (Weigel 1962, Brattstrom 1953) and Texas (Holman 1965, Slaughter and McClure 1965). A supposed Pleistocene specimen from Germany (Brunner 1956) has been shown to be the parasphenoid of a fish (Estes 1969b). *A. jepsoni* is found in the upper Paleocene of Montana and *Proamphiuma cretacea* in the Upper Cretaceous of the same state (Estes 1969b).

RELATIONSHIPS. Familial relationships of the Amphiumidae are discussed below (see Conclusions). Goin (1936) produced evidence casting doubt on the validity of recognizing *A. tridactylium* as distinct from *A. means*. He suggested that the former be recognized as a subspecies of *A. means*, but Salthe (1973a,b) has rejected this. Evidence is not conclusive, but the only characters serving to distinguish the two "species" are coloration and number of toes. The two forms are otherwise the same, occupy adjacent but continuous ranges, and produce so-called hybrids (Goin 1936). The validity of specific status for *A. tridactylium*, although possible, cannot be said to be probable. *Amphiuma pholeter*, a dwarf one-toed species, is known from a few localities in northwestern Florida (Neill 1964).

REMARKS. Only the anteriormost trunk vertebrae (the first three, four, or five), in the region of the pectoral girdle, bear ribs, which are very small. There are approximately 60 myomeres between the limb girdles, correlating with the great length of the trunk. Movement is anguilliform, with the limbs moving in an active, co-ordinated manner as the animal progresses over the substrate. The pectoral limbs appear to help in changing direction (Shufeldt 1883) and "the hindlimbs are active in checking onward movement" (Baker 1945, p. 73). It appears, therefore, that the limbs are not "degenerate," but reduced and functional.

The basic pattern of the myomeres is very like that of hynobiids and ambystomatids and readily derivable from either. However, they have become more highly folded, in a manner comparable to, but different from, the condition in teleost fishes (see Nursall 1956).

Epaxial musculature (see Figs. 28 and 29).- Auffenberg (1959) described the epaxial musculature of *Amphiuma*. However, owing to the fact that many of his observations are at variance with mine, redescription and correction are necessary. According to Auffenberg (1959, p. 256) there are "many [muscle] fibers attaching to the internal surface of the skin." This is incorrect; instead there is a system of tough, seemingly random fibers of connective tissue binding the skin to the musculature. There are no muscle fibers evident between the skin and the trunk musculature and, indeed, they would serve little purpose in such a position.

Auffenberg attempted to distinguish "tracts" of muscle fibers in the *dorsalis trunci*, especially as they related to the vertebrae. However, at least from a functional and comparative point of view, the important point is not these tracts, which are in a sense artificial, but the total myomere in relation to the vertebrae and the other myomeres. That is, although many of Auffenberg's described tracts are present, their delineation is somewhat misrepresentative. Further, the descriptions and figure (Auffenberg 1959, fig. 2) of the axial myosepta are almost wholly incorrect. Fibral orientations and the distributions of flexures in the myomeres are somewhat difficult to elucidate. However, with careful dissection "clear demarkations between muscle masses" are readily apparent (contra Auffenberg 1959, p. 253).

According to Auffenberg (1959, p. 264) "the specializations in *Amphiuma* can more easily be derived from the primitive condition in *Necturus* than can those of *Siren*." In fact, *Amphiuma* is most readily derived from a hynobiid or ambystomatid structural ancestor, *Necturus* is highly derived in its epaxial musculature, and *Siren* is much closer to *Necturus* in the structure of the *dorsalis trunci* than *Amphiuma* is to either of these (compare the figures and descriptions of the three genera provided below).

In a manner somewhat similar to teleosts (see Nursall 1956), the myomeres show development of anterior and posterior V-shaped flexures. There are two anterior flexures in each myomere of the *dorsalis trunci*. The more medial primary flexure is probably homologous with the single anterior flexure described in hynobiids, based on positional relationships. The secondary anterior flexure is shorter, does not extend as far into the next anterior myomere, and attaches to the transverse process below. This accessory flexure was presumably developed owing to the demands of anguilliform locomotion. The posterior flexure is seemingly homologous to the posterior portion of the main body of the myomere in ambystomatids. It has, however, undergone considerable increase in length.

Each of the three epaxial flexures extends deep into the neighboring myomeres, extending each myomere across several intervertebral joints. Muscle fibers fan from the flexures, concentrating force in these areas. This development of "forward and backward-pointing cones," with cones fitting within cones (Alexander 1968, p. 98), is less pronounced than in sharks or teleosts. However, it presumably serves the same function in fish and salamander, allowing each myomere to affect several vertebrae. This may decrease lateral bulging when the trunk muscles contract, smooth the action over several vertebrae, and/or divide the muscle fibers into numerous interseptal groups, providing more power than would a long undivided band. The system probably also causes force to be concentrated away from the vertebral column, decreasing stress on the intercentral joints (see also Nursall 1956).

The attachments of the myosepta to the vertebrae are closely correlated with topographic features on the transverse processes, neural arches, and centra. This differs significantly from the situation in other urodeles, although sirenids (q.v.) are closely convergent in this regard. Each septum extends forward from the anterior surface of the posterolateral flange of the hyperapophysis, along an indistinct ridge on the neural arch next to the neural crest. Then, posterolateral to the articular surface of the prezygapophysis, the septum reverses direction and extends posterolaterally along the large postzygapophyseal ridge to the posterolateral border of the postzygapophysis. From this point the attachment proceeds anteriorly along the edge of the postzygapophysis until the transverse process is reached. The septum runs laterally along the rear edge of the transverse process and hence out into the muscle mass (see also the description of the trunk vertebrae of *Amphiuma* and Fig. 4).

In addition to this main septum there is a relatively small septum attaching to the posterolateral surface of the hyperapophysis and proceeding posteriorly lateral to the neural crest. This provides attachment for the muscle fibers of the hyperapophyseal muscle. In contrast to hynobiids and ambystomatids, the hyperapophyseal septum is oriented vertically. Dorsal to the neural crest the septum is a backwards continuation from the septum that forms the boundaries of the myomere. Unlike the more primitive condition in hynobiids and ambystomatids, the septum attaches ventrally to the neural arch and dorsally to the superficial fascia, which bounds the *dorsalis trunci*. Nevertheless, derivation from the ambystomatid pattern is simple (compare, e.g., *Ambystoma tigrinum*).

Within each myomere muscle fibers are aligned approximately parallel to the midline, but with deviations (especially in the more medial areas) where necessary to exert optimal pull on associated septa. Pinnate and fan-shaped muscle systems are thus formed within the myomeres (see also Hildebrand 1974). The detailed arrangements of the muscle fibers and septa of the *dorsalis trunci* are shown diagrammatically in Figures 28 and 29.

Hypaxial musculature (see Figs. 28 and 30).- According to Auffenberg (1968, p. 184) "the deeper portions of the subvertebralis complex are similar in all the genera [of salamanders] for which the myology is known, except for the strong series of fibers attaching on the basipophyses [sic] in *Amphiuma*." This statement is incorrect, the *subvertebralis* being quite different amongst urodeles. Furthermore, the Hynobiidae, Cryptobranchidae, Ambystomatidae, and Amphiumidae form a homogeneous group with the same ground plan of axial musculature. *Amphiuma* differs from the other members of this group (named the Archeocaudata below) only in the accentuation of certain aspects of the *subvertebralis*.

The epaxial musculature is separated from the hypaxial by the transverse process and a thin horizontal septum. However, the two parts combine to form a single functional unit distal to the vertebral column. The septal pattern of the *subvertebralis* is developed in a manner analogous to that described for the *dorsalis trunci*, but as a reversed image. The subcentral keel of each vertebra may be considered the ventral functional analogue of the neural crest, whilst the anterior basapophyses correspond to the (posterior) hyperapophyseal plate (see Fig. 4). The septa of the *subvertebralis* relate to the subcentral keels and basapophyses as do the epaxial septa to the neural crests and hyperapophyses, although the hypaxial system is somewhat simpler than the dorsal.

From the posterolateral edge of each anterior basapophysis a septum extends posteriorly and slightly laterally along the ventral surface of the centrum. At the lateral edge of the posterior cotyle this attachment reverses to extend anterolaterally along a faint groove on the under surface of the ventral lamella to the latter's anterior edge. The septal attachment then proceeds along the anterolateral surface of the lamella to the tip of the transverse process laterally, and hence into the distal musculature. The shape of the ventral lamella correlates exactly with the sharpness of the angle of the anterior flexure of the subvertebral myomere. In the anterior part of the column, immediately postcranially, the flexures are very obtuse. This correlates with the small ventral lamellae sweeping very gently and smoothly posteriorly (see description of the vertebral column of *Amphiuma*). However, throughout most of the column the transverse processes are produced anteriorly into a plate, correlating with the greater acuteness of the anterior flexures.

As in hynobiids and ambystomatids, anterior basapophyseal muscles are present, although greatly accentuated. The muscle fibers attaching to the basapophyseal septum are short and extend obliquely anteriorly. The medial series of fibers orient anteromedially between the subcentral keel and the basapophyseal septum, the lateral series extends anterolaterally between the basapophyseal septum and the septum of the posterior flexure of the next anterior myomere. Well-developed posterior flexures are present and neomorphic anterior flexures are situated lateral and anterior to these in each myomere. The main body of each myomere is elongated and slants posterolaterally from the apex of the anterior flexure (see Fig. 30).

The septal patterns of the epaxial and hypaxial myomeres are thus developed in a very similar manner, but with the system of flexures reversed and an extra flexure in the epaxial portion. The *subvertebralis* is bound by very tough connective tissue, which is continuous with the myosepta extending to the peritoneal surface. This layer, plus the partial overlap of the myomeres, makes the actual pattern more complex than the semi-diagrammatic figures might indicate.

In addition to the system of septal flexures described in association with the vertebrae, a large mass of musculature is developed distal to the vertebral column. This is composed of epaxial and hypaxial fibers, divided one from the other by the horizontal septum. By far the greatest proportion of trunk musculature is intermyoseptal, to use Auffenberg's (1959) terminology. The intermyoseptal muscle fibers act indirectly on the vertebrae.

Except for the atlas and more posterior caudal vertebrae, exits for the spinal nerves are intervertebral. Each nerve passes laterally and slightly posteriorly through the *subvertebralis* into the lateral abdominal musculature. The nerves are not exposed to the peritoneal cavity.

Lateral abdominal musculature (see Figs. 31 and 32).- The lateral abdominal musculature of *Amphiuma* is unique in having become completely separated from the epaxial and hypaxial myomeres. This portion of the axial musculature attaches laterally to the myomeres by means of tough connective tissue, contrasting with other urodeles in which only the *o. e. superficialis* and *transversus* are generally separate from the *subvertebralis*. My dissections show Maurer's (1911) studies to be substantially correct, although further details may be added.

The lateral abdominal musculature of *Amphiuma* is amazingly similar to that of *Rhyacotriton* and, to a lesser extent, *Dicamptodon*. This is of interest as regards the origins of the Amphiumidae, which are discussed more fully below. Edwards (1976) reported similarities in the patterns of spinal nerve exits in amphiumids and dicamptodontines. The additional resemblance in the lateral abdominal musculature is suggestive of close relationship. This can be interpreted in two ways: either these salamanders are derived from a common ancestor, or they represent derivation from a primitive grade and are, therefore, not especially closely related (see below).

The *obliquus externus superficialis* is a narrow band extending only a short distance ventrally. Its muscle fibers align posteroventrally at a slight angle and the sheet of musculature is a continuous lateral band, not divided by myosepta. The *o. e. profundus* is not visible until removal of the *o. e. superficialis* and dorsal extension of the *rectus abdominis*. The fibers of the *o. e. profundus* extend posteroventrally between adjacent myosepta at an angle little displaced from the horizontal. Ventrally it merges with the fibers of the main part of the *rectus abdominis*.

Deep to this layer is located the *obliquus internus*. This does not extend as far dorsally as do the fibers of the two layers of the external oblique. The fibers of the *o. internus* extend anteroventrally in the dorsal part, but midway down come to align horizontally. The *o. e. profundus* and *o. internus* blend together ventrally to form the main portion of the simple *rectus abdominis*. The muscle fibers here extend anteroposteriorly between the segmenting myosepta. Externally the *rectus abdominis* gives rise to a thin layer of muscle fibers that align anteroposteriorly and cover the *o. e. profundus* in the area below the *o. e. superficialis*. This is similar to the condition of dicamptodontines.

The deepest part of the lateral abdominal musculature, next to the peritoneal cavity, is the *transversus*. This layer extends dorsoventrally from just below the upper limit of the *o. e. profundus* to almost the medial border of the *rectus abdominis*. Its muscle fibers extend anteromedially at an angle barely displaced from the vertical. Excepting the *o. e. superficialis*, all layers of the lateral abdominal musculature are transversely segmented by myosepta, which are in line with the myosepta forming the epaxial myomeres, although not connected to them. The segments thus formed are inclined such that the external edge of a given myoseptum is further anterior than is the internal (deep) edge.

iv) Family Ambystomatidae Hallowell 1857

a) Subfamily Dicamptodontinae Tihen 1958

Dicamptodon ensatus (Eschscholtz 1833)

RANGE. Found from "southwestern British Columbia to Santa Cruz County, California . . . in humid coastal forests, and in the Rocky Mountains of Idaho and Montana" (Anderson 1969, p. 761.1).

HABITAT. Larvae are found in streams and creeks, while adults occur "under logs, bark, rocks, and other objects, usually in damp situations not far from a permanent stream or in the water" (Stebbins 1962, p. 50). Neotenic individuals are known and the species *Dicamptodon copei* is almost totally paedogenic (Nussbaum 1976).

FOSSIL RECORD. None for this species, but Peabody (1954) described trackways from the Paleocene as a new genus *Ambystomichnus*; these tracks show resemblances to those made by living *Dicamptodon ensatus*. Tihen (1958) classified *Ambystomichnus* along with *Dicamptodon* in the

Dicamptodontinae. A lower Pliocene trackway in California has been referred to *Dicamptodon* by Peabody (1959).

RELATIONSHIPS. Tihen (1958) believed *Dicamptodon* to be an early derivative of ambystomatid stock and not especially close to *Rhyacotriton*. Regal (1966) classified both these genera in a single subfamily, however, suggesting *Dicamptodon* to be "advanced" over *Rhyacotriton*. Edwards (1976), largely on the basis of the relationships of spinal nerves to vertebrae, created a new family Dicamptodontidae for *Dicamptodon*, *Rhyacotriton*, and the fossil scapherpetontids. My interpretation, argued below, is that *Rhyacotriton* and *Dicamptodon* are closely related and to be classified in a single subfamily within the Ambystomatidae. The precise relationships of the scapherpetontids are not well enough understood to support Edwards' (1976) suggestion, although it is possible that he is correct.

REMARKS. These are large (to 12 inches total length), robust salamanders. The limbs are powerful, with the hindlimbs much larger than the fore. In external shape and proportions *Dicamptodon* is similar to *Ambystoma*, but there are osteological and myological distinctions (see below and Tihen 1958). There are generally 12 costal grooves. Larval *Dicamptodon* have elongate, narrow premaxillary spines, which are modified in the adult to very broad plates. It is, therefore, not correct to interpret the adult condition as a primitive, hynobiid-like, feature. It is rather an autapomorphy (Hennig 1966). Tihen (1958) interpreted the tendency to ossify parts of the hyobranchial apparatus as a primitive feature. Comparison with hynobiids, crytobranchids, and other ambystomatids shows this to be a secondary development (see also Krogh and Tanner 1972).

Epaxial musculature (see Figs. 33 and 34).- The *dorsalis trunci* of the adult and larva is very thick and extends laterally beyond the ends of the ribs. Unlike the species of *Ambystoma* described below, the anterior flexures lack medial portions. Rather, they join to their neighbours of the opposite side. These anterior flexures are very thin dorsoventrally, being composed of only a few layers of muscle fibers. In this, as in other features, *Dicamptodon* shares derived character states with *Rhyacotriton* (q.v.), indicating they are more closely related than generally accepted. In adults, the anterior flexures are small in the anterior region of the trunk, increasing in their forward extent back along the column. In larvae, they extend forward a notably greater distance, almost to the hyperapophysis of the vertebra in front of the anterior vertebra of the pair spanned by their myomere. Muscle fibers extend anterolaterally within each anterior flexure, forming an acute angle with the median in adults. In larvae there is a single layer of superficial fibers running anterolaterally at a more obtuse angle. The topmost fibers are underlain by a series extending much more acutely.

The main body of each myomere extends posterodorsally from between adjacent vertebrae and ribs. Most of the fibers extend anterolaterally as do those of the anterior flexure. In larvae, there is a single layer of fibers running anteroposteriorly on the lateral surface of each myomere. These are applied over the anterolateral fibers. No horizontal septum divides the *dorsalis trunci* from the hypaxial musculature in adults, although one is present in larvae. In larval individuals there is a large mass extending posteromedially from the rear edge of each anterior flexure into the next posterior myomere. There appears to be no direct attachment of this deep posterior flexure to the vertebral column. Discrete, although large, posterior septa extend from the posteromedial surface of the main body of each myomere in adults. These extend posteromedially to join to the lateral edge of the hyperapophyseal spine of the vertebra just posterior to the last in the pair spanned by the myomere. They are present in the pectoral region, but reach maximum development posteriorly. Based on appearance and positional relationships, these posterior septa are almost certainly homologous to the deep posterior flexures described in plethodontids.

Small hyperapophyseal muscle blocks are present. These arise from septa that attach to the posterolateral borders of each hyperapophysis, one pair of septa per hyperapophysis.

Hypaxial musculature (see Figs. 33 and 34).- The *subvertebralis* of larval and adult *Dicamptodon* is basically similar, and the pattern is conformable to that of hynobiids and other ambystomatids. Anterior basapophyseal muscles are present and well developed. Those of the opposite side do not meet medially. Long, slender transverse process flexures extend back from each transverse process, and there are short, very broad anterior flexures. In larvae a short septum extends forward from each anterior flexure, paralleling the transverse process flexure of the next anterior myomere. In adults this develops into a long, broad septum, which attaches medially to the connective tissue about the intercentral joint and to the internal septum of each transverse process flexure. Fibers extend anteromedially from the dorsal surface of each anterior flexure septum to attach to the next forward transverse process flexure, and anteriorly and slightly laterally from the ventral surface to form the anterior flexure of the next anterior myomere. Most ventrally there is a single layer of muscle fibers that obscures the features just described.

In both larval and metamorphosed individuals the main body of each myomere is inclined anteriorly, such that the myomere overlaps its anterior neighbour. The *subvertebralis* is thick ventral to the ribs, especially in metamorphosed specimens. Muscle fibers extend anterolaterally in the main body of the myomere, but those running directly between adjacent ribs are aligned posterolaterally. The anterolateral fibers are continuous with the *obliquus internus*, whereas the posterolateral group blends with the *o. e. profundus*.

Spinal nerves exit intervertebrally in the trunk, a condition also seen in *Rhyacotriton*, amphiumids, and cryptobranchoids, but differing from other ambystomatids. However, the caudal nerves exit intravertebrally (see also Edwards 1976). In metamorphosed specimens the spinal nerve is buried in musculature throughout its length. In larvae the nerves are exposed to the peritoneum for a short distance before extending external to the *transversus*.

Lateral abdominal musculature (see Figs. 33 and 34). The lateral abdominal musculature is basically similar in adult and larva. It shows certain resemblances to the conditions in *Amphiuma*, *Rhyacotriton*, and (to a lesser degree) plethodontids, but differs from that of hynobiids and ambystomatines. The situation in *Dicamptodon* and *Rhyacotriton* is probably a shared-derived character, indicating monophyletic (sensu Simpson 1961) derivation of the two (see Conclusions).

The *obliquus externus superficialis* is relatively thick and not divided by myosepta. It is narrow dorsoventrally, slightly overlapping the epaxial musculature above and the *rectus abdominis* below. The muscle fibers extend posteroventrally. Dorsally and ventrally the *o. e. superficialis* attaches to a tough fascia, which surrounds the rest of the trunk. Larvae differ from this in that the *o. e. superficialis* does not extend over the myomeres of the *dorsalis trunci*.

A narrow *rectus lateralis* is present in larval, but not in adult individuals. In both there is developed a thick *o. e. profundus* and *o. internus*, which are continuous with the subvertebral musculature dorsally. These two layers are divided by myosepta and blend together ventromedially to form the *rectus abdominis*. The latter is very broad, but simply constructed — the adult being foetalized with respect to its retention of this simplicity. The *r. abdominis* also has a unit of anteroposteriorly directed muscle fibers that extend up over the external surface of the *o. e. profundus*. In larval individuals the latter unit is divided from the epaxial musculature by a distinct septum, which is lacking from metamorphosed specimens.

The larval *transversus* is relatively wide, extending up under the *subvertebralis*, at which point it is divided by myosepta. This is similar to certain species of *Ambystoma* (e.g., *A. maculatum*). In the adult the myosepta of the lateral parts of the subvertebral myomeres come to be deflected posteriorly. In this area the *transversus* is very thick and forms a functional part of the *subvertebralis*. The myosepta dividing the *transversus* dorsally have a more pronounced posterolateral alignment than those parts external to this (the latter being the part dividing the *o. e. profundus* and *o. internus* segmentally). In comparison to the larval condition, the *transversus* of the adult is thick and relatively narrow dorsoventrally. Except for the most dorsal portion, it is not segmented by myosepta.

Rhyacotriton olympicus (Gaige 1917)

RANGE. Found "from the Olympic Peninsula of northwestern Washington southward to Mendocino County, California, in humid coastal [coniferous] forests" (Anderson 1968, p. 68.1).

HABITAT. The genus is adapted to mountain brook life and has reduced lungs and gills. It is found "in and near small, rapidly flowing, well-shaded, permanent streams," often under rocks (Stebbins 1962, p. 56).

FOSSIL RECORD. None known.

RELATIONSHIPS. Gaige (1917) described this species as a hynobiid, *Ranodon olympicus*. Dunn (1920) subsequently erected the genus *Rhyacotriton* for the species and noted its similarity to *Ambystoma* and *Dicamptodon*. However, at that time he saw no necessity for classifying hynobiids and ambystomatids in separate families. Eaton (1933, 1934) believed *Rhyacotriton* to share streptostyly with *Ambystoma gracile* and *A. macrodactylum*, which was claimed to indicate derivation of *Rhyacotriton* from *A. macrodactylum* or a similar species. Subsequent workers (e.g., de Villiers 1938a,b) questioned the presence of streptostyly and my observations indicate its occurrence to be doubtful.

Tihen (1958) classified *Rhyacotriton* in a separate subfamily, the Rhyacotritoninae. He (1958, p. 22) noted that the genus shared several character states with *Dicamptodon*, but that these were primitive and that each genus "has so many unique characters that the two are no more similar to each other than to the remainder of the family." Tihen (ibid.) went on to state that: "All of these resemblances represent apparently primitive features; none of the specialized characteristics of either form are found in the other. The points of similarity do not, then, denote any close relationship between the two, but simply indicate that the lines leading to these two forms were derived from the ancestral proto-Ambystomatidae at an early stage, prior to the development of the specializations characterizing the remainder of the family." Krogh and Tanner (1972), although noting resemblances in the hyobranchia of *Rhyacotriton* and *Dicamptodon*, also concluded that they were independent derivations from proto-ambystomatid stock.

Regal (1966) classified *Rhyacotriton* with *Dicamptodon* in the Dicamptodontinae, suggesting that it "could be classified with a group of hypothetical adaptive types in the Ambystomatoidea [ambystomatids and plethodontids]" (p. 405). He believed *Rhyacotriton* to be similar to the ancestral plethodontid in its reduced lungs and prominent inter-premaxillary fontanelle. Worthington and Wake (1971) noted the apparent lack of derived characters shared by *Rhyacotriton* and *Dicamptodon* and argued against uniting these taxa on the basis of primitive characters alone. Regal's (1966) suggestion of plethodontid relationships to *Rhyacotriton* is noteworthy in light of the evidence presented below.

Most recently, Edwards (1976) suggested a major revision in classification. His family Dicamptodontidae is composed of three subfamilies: the Rhyacotritoninae (*Rhyacotriton*), the Dicamptodontinae (*Dicamptodon*), and the Scapherpetontinae (*Scapherpeton* and *Lisserpeton*). This reclassification is based on patterns of spinal nerves and their relationships to the vertebrae. As argued below, it is here concluded that *Rhyacotriton* and *Dicamptodon* are to be included in a single subfamily within the Ambystomatidae, as proposed by Regal (1966).

REMARKS. The general shape of the head and trunk is somewhat similar to that of the eastern large plethodons (see below). This species is made up of relatively small animals, with individuals reaching four inches total length being large. There are usually 14 costal grooves. The trunk is robust, but not thickened, and the tail is relatively high and short. The limbs are robust, but small.

Epaxial musculature (see Fig. 35).- The *dorsalis trunci* is divided into myomeres of a pattern similar to that of *Dicamptodon*. A single row of large glands extends down the trunk medially (see Worthington and Wake 1971). Anterior flexures are as in *Dicamptodon*, with the medial portions lacking. That is, muscle fibers do not fan forward within each flexure, but extend only anterolaterally from the midline. Unlike *Dicamptodon*, however, no posterior extensions of the myomeres appear to be present.

Hypaxial musculature (see Fig. 35).- The *subvertebralis* of smaller *Rhyacotriton* differs significantly from that of *Dicamptodon* and *Ambystoma*. Young, although metamorphosed, specimens (snout/vent length of 40 mm) lack anterior basapophyseal muscles. Narrow posterior flexures are present next to the centra. These are modifications of the transverse process flexures developed owing to failure of full anterior basapophyseal muscles to appear. There are no posterior basapophyses present on the vertebrae and the posterior flexures are integral parts of the *subvertebralis*. In larger specimens, a thin band of muscle fibers extending posterolaterally from each centrum to the paralleling septa converts this system into the anterior basapophyseal type of musculature seen in the other ambystomatids.

Each subvertebral myomere has a small, forwardly projecting septum at the forward apex. Muscle fibers fan anteriorly from this septum. The main body of the myomere is thick, dropping more or less straight down from between adjacent ribs. In this main portion muscle fibers extend anterolaterally within each myomere. At the lateral edge of each half of the *subvertebralis* the *transversus* is underlapped. In this relationship to the *transversus*, and in overall structure, the *subvertebralis* resembles the condition of *Plethodon* very closely.

Spinal nerves exit intervertebrally in the trunk region (except for the atlas), passing laterally through the subvertebral myomeres. They are exposed to the peritoneal cavity for the lateral one third of the *subvertebralis*. From here they extend between the *transversus* and *obliquus internus*, each nerve paralleling a myoseptum. In the caudosacral and caudal regions the nerves exit intravertebrally (see also Edwards 1976).

Lateral abdominal musculature (see Fig. 35).- As in *Dicamptodon* the *obliquus externus superficialis* is a narrow, relatively thick band not segmented by myocommata. The muscle fibers extend posteroventrally at an angle little displaced from the vertical. *Rhyacotriton* differs from *Dicamptodon* in that the *o. e. superficialis* does not extend over the epaxial myomeres or the *rectus abdominis*, but is confined to the area between the two. A further difference is the presence of a narrow *rectus lateralis*, a muscle apparently lacking in adult *Dicamptodon*.

The *o. e. profundus* and *o. internus* are present and developed as in *Dicamptodon*. Ventromedially these two units blend together to form the *rectus abdominis*, which is developed as in *Dicamptodon*. The *transversus* does not extend onto the undersurface of the *subvertebralis*. Rather, it arises inside the subvertebral myomeres in association with the ribs. From here it extends anteroventrally against the inner surface of the *o. internus*. The *transversus* is not divided by myocommata.

Rhyacotriton shows remarkable similarity in the lateral abdominal musculature to the condition in *Plethodon* and, more especially, *Amphiuma*.

b) Subfamily Ambystomatinae Hallowell 1857

Ambystoma Tschudi 1838

RANGE. Found throughout North America, except for northern Canada, the southern part of Florida, the southern Rocky Mountains in the United States, Baja California, and the west coast of Mexico (see Tihen 1969).

HABITAT. Very diverse, see under individual species below.

FOSSIL RECORD. Four fossil species of *Ambystoma* are presently recognized: *A. tiheni* from the lower Oligocene of Saskatchewan, placed in the *A. opacum* species group of Tihen (1958) by Holman (1968), to which it bears little resemblance (see above). It is probably a member of the *A. macrodactylum* group described below. *A. minshalli* Tihen and Chantell 1963 is known from the Miocene of Nebraska, Colorado, and South Dakota (Chantell 1971, Tihen 1969) and assigned to the *A. maculatum* species group of Tihen (1958). It would fit as well or better in the *A. macrodactylum* group (see below). *A. kansense* comes from the middle Pliocene of Kansas and is close to the *A. tigrinum* species group (Adams and Martin 1929, 1930, Taylor 1941, Tihen 1969). *A. hibbardi* Tihen 1955 from the upper Pliocene of Kansas is very close to *A. tigrinum*. Remaining fossil *Ambystoma* are assignable to living species and are discussed below.

RELATIONSHIPS. Relationships within the genus *Ambystoma* are discussed below in the individual accounts of the species. Those of the genus are considered in the Conclusions section.

Ambystoma macrodactylum Baird 1849

RANGE. The exact range of this species is uncertain, but specimens are known from northern California, throughout the states of Oregon and Washington, much of Idaho, Vancouver Island, and southern British Columbia. It has also been collected from the northern part of British Columbia, the Rocky Mountains of southern Alberta, and Santa Cruz County, California (see Ferguson 1961, 1963).

HABITAT. Found in a wide range of environments, "from sea level to 9000 feet elevation, inhabiting sagebrush semidesert and all intermediate vegetation types up to alpine meadows" (Ferguson 1963, p. 4.1). Neoteny is not known and adults are secretive, found under logs and other kinds of surface litter.

FOSSIL RECORD. None for this species, but *Ambystoma tiheni* and *A. minshalli* may be related (see below).

RELATIONSHIPS. Eaton (1933, 1934) suggested that *A. macrodactylum* could serve as an ancestor to *Rhyacotriton*. This conclusion, based on the supposed common occurrence of streptostyly, has been rejected by subsequent workers (de Villiers 1938a,b, Tihen 1958). Tihen (1958) placed *A. macrodactylum* along with *A. gracile* in the *A. maculatum* species group, although he did not consider the two western species to be closely related. He suggested that each was derived from separate ancestry from within the *A. maculatum* group, each reaching the west via a northern route from Appalachia at a different time.

If, as here suggested, the *A. maculatum* group of Tihen (1958) includes the most primitive living species of *Ambystoma*, it is more likely that *A. macrodactylum* and *A. gracile* are relict representatives of basal *Ambystoma* stock. In the structure of the vertebral column and associated trunk musculature, *A. macrodactylum* is decidedly primitive, closely resembling hynobiids, but somewhat divergent with respect to the eastern representatives of Tihen's (1958) *A. maculatum* group.

There is no special reason to consider *A. macrodactylum* or *A. gracile* as close to the eastern members of the *A. maculatum* group. It is probably best to separate them into a distinct species group, representative of basal *Ambystoma* stock. This is the *A. macrodactylum* species group, including the living *A. macrodactylum* and *A. gracile* and perhaps the fossil species *A. tiheni* and *A. minshalli*. Tihen's (1958) suggested sequence for the phylogeny of the genus *Ambystoma* is improbable (see Conclusions). In certain features the new species group shows resemblance to *Dicamptodon* and *Rhyacotriton* (see descriptions provided, plus Eaton 1933, 1934). The resemblances shared with *A. maculatum* and its allies are, therefore, owing to retention of primitive characters and cannot be used to support special relationship.

REMARKS. The trunk is long and, for an ambystomatid, quite slender (compare *A. maculatum*). There are 12 or 13 costal grooves, with occasional counts as high as 14 (Stebbins 1962). The tail is long and laterally compressed, especially posteriorly. Limbs are fairly robust and powerful with elongate toes. The head is slender in comparison to other *Ambystoma*.

Epaxial musculature (see Fig. 36).- The *dorsalis trunci* is similar to that of *A. jeffersonianum*, but with a proportionally greater mass. The anterior flexures are long and thin, but end bluntly. Muscle fibers within each flexure fan anteriorly from a forwardly projecting septum on the apex of each flexure.

The main body of each myomere is composed of fibers extending anteroposteriorly. The main body extends distal to the ribs a relatively greater distance than in either *A. maculatum* or *A. jeffersonianum*, owing to the shortness of the ribs in *A. macrodactylum*. Deep posterior septa are present in the most posterior region of the trunk. However, in contrast to the situation in *A. jeffersonianum*, they are not so much associated with the main bodies of the myomeres as with the anterior flexures (i.e. they are situated further anteriorly on each myomere). Each slip attaches to the neural arch of the following vertebra just medial and anterior to the point at which the transverse process meets the neural arch.

Hypaxial musculature (see Fig. 36).- The *subvertebralis* is of basic ambystomatid plan, but somewhat modified. The more superficial muscle fibers fan anteriorly from the apex of each anterior flexure and the associated septum of the latter. Lateral to this, in the main body of each myomere, fibers run anterolaterally, the most lateral ones being situated between the *transversus* (internally) and the *o. e. profundus* (externally). Each anterior flexure is provided with a broad, forwardly projecting septum, such as in *Dicamptodon*. Muscle fibers attach dorsally and ventrally onto this septum. The dorsal fibers extend anteriorly into the next anterior flexure, ventral fibers extend anterodorsally onto the transverse process flexure of the next anterior myomere. Transverse process flexures are relatively short and narrow, with relatively long, posteriorly directed septa at their apices. Unlike the condition in *A. maculatum*, these posterior flexures are curved medially so as to cover most of the associated anterior basapophyseal muscles. These latter are developed as in the other species of *Ambystoma*.

In the main body of each subvertebral myomere a thin ventral layer of muscle fibers extends anterolaterally. Dorsal to these the fibers run posterolaterally, forming the intercostal series. This group extends ventrally, becoming the *o. e. profundus* of the lateral abdominal musculature. The ventral rib-bearers are provided with a horizontal, short septum that extends posteriorly. These septa provide extra sites of attachment for the intercostal muscle fibers and were not observed in other adult ambystomatids.

Spinal nerves, excepting those in association with the second cervical, are intravertebral in their exits and have the same positional relation to the musculature as described in *A. maculatum* and *A. jeffersonianum*.

Lateral abdominal musculature (see Fig. 36).- The layers of this system are distinctive amongst adult ambystomatids here described. Externally the *o. e. superficialis* is a lateral band extending between the limb girdles. Transverse septa divide this unit and the muscle fibers run posteroventrally between them. Dorsally, the *o. e. superficialis* barely meets the epaxial myomeres, exposing the *rectus lateralis* in places. Ventrally, the *o. e. superficialis* extends to the area where the *o. e. profundus* and *rectus abdominis* merge.

A distinct *rectus lateralis* is present deep to the *o. e. superficialis* and ventral to the epaxial myomeres. This unit is, presumably, a neotenic character. As noted, the *o. e. profundus* is a direct continuation of the *subvertebralis*. In lateral view its fibers extend posteroventrally at an angle slightly displaced from the horizontal. Ventrally it merges more or less indistinguishably into the *r. abdominis*. There is no *obliquus internus* in the adult, although a portion of the *subvertebralis* extends a short distance between the *transversus* and *o. e. profundus*. The most dorsal part of the *transversus* is applied against the undersurface of the *subvertebralis*. Myosepta segment the *transversus* for approximately its dorsal two thirds. The muscle fibers extend anteroventrally at a relatively steep angle, little displaced from the vertical. Ventrally the *transversus* does not quite reach to the division between the two parts of the *r. abdominis*.

The *rectus abdominis superficialis* is continuous with the *o. e. profundus* dorsally, and composed of fibers extending anteroposteriorly. The *r. a. profundus* is composed of a single layer of muscle fibers running anteromedially. It is located between the *o. e. profundus* and the *transversus*, as well as being internal and lateral to the *r. a. superficialis*. The *r. a. profundus* is less differentiated than in hynobiids, *A. maculatum*, or *A. jeffersonianum*, being presumably foetal in this regard.

Ambystoma gracile (Baird 1859)

RANGE. Found along the Pacific coast of North America from the Alaskan panhandle southwards to northern California, and on Vancouver Island, British Columbia (Snyder 1963, p. 6.1).

HABITAT. "Confined to coastal forests west of the Cascade Divide, but occurs from sea level to timberline." Adults are found "beneath logs, in leaf litter, [and] stumps . . . in deciduous or coniferous forests; larval life is confined to ponds and lakes" (Snyder 1963, p. 6.1). Neoteny is common, with populations from higher altitudes being composed largely of neotenic individuals (Snyder 1956).

FOSSIL RECORD. None known.

RELATIONSHIPS. Grouped by Tihen (1958) in the *A. maculatum* species group, but here considered to be most closely related to *A. macrodactylum*, the two forming a distinct species group (see discussions under *A. macrodactylum*).

REMARKS. Only larvae of *A. gracile* were available for dissection. They are of typical *Ambystoma* structure with a relatively broad, depressed head. The trunk is robust, with 11 costal folds, as in *A. tigrinum*. The lateral abdominal musculature is thick and the belly large. The tail tapers to a fine point, is highly compressed laterally, and provided with a large dorsal and ventral fin. Skeletal material of adults available to me have a distinct postdental process on the vomers. Tihen (1958) claimed this process to be lacking in *A. gracile*, so there may be individual variability in this character.

Epaxial musculature (see Figs. 37 and 38).- The *dorsalis trunci* is thick, rising above the vertebrae so that the hyperapophyses are deeply buried (compare larval *A. tigrinum*). There is a median groove between the two halves of the epaxial musculature. Anterior flexures extend only a short distance forward. In the anterior part of the trunk the medial parts of these flexures are not visible in external dorsal view. However, as the sacral region is approached, these portions become evident.

The main body of each myomere rises steeply, with only a slight amount of posterior inclination. Myomeres in the anterior region are more steeply inclined than those further posterior. Muscle fibers extend anterolaterally and anteroventrally within the myomeres. Each hyperapophysis gives rise to a pair of hyperapophyseal muscles, the septa of which insert on the cartilaginous cap. These muscles are narrow from side to side, but originate along the entire length of the neural arch of the next posterior vertebra.

Hypaxial musculature (see Fig. 38).- The *subvertebralis* is situated laterally on either side of the centra, as in larval *A. tigrinum*. The centra are not surrounded by musculature ventrally. Anteriorly the fifth and sixth subvertebral myomeres are transitional between the nuchal and pectoral trunk musculature and that of the trunk proper. The third, fourth, and fifth myomeres are associated with the pectoral girdle and are relatively narrow anteroposteriorly. The medial pull of these myomeres is concentrated on the posterior cotyles of the centra, rather than on the anterior edges as in the more posterior regions of the trunk.

Cleared and stained larvae show the atlas and first three trunk vertebrae to be provided with distinct posterior basapophyses. All of the remaining trunk vertebrae have some trace of anterior basapophyses, at least in larger larvae. Anterior basapophyseal muscles are maximally developed in the midtrunk region, just posterior of the pectoral girdle. Here they are elongate, extending well forward along the sides of the centra. At the rear of the trunk, as the sacrum is neared, these muscles become progressively smaller, owing mainly to decrease in their anterior extent. In the immediately presacral myomeres, basapophyseal muscles are very small or lacking. They may be present on only one side of the column in this area. In the sacral region, basapophyseal muscles and transverse process flexures are lacking. Anterior basapophyseal muscles are well developed in larger larvae, which invariably have distinct anterior basapophyses on the centra, as do metamorphosed individuals. Transverse process flexures extend back from the ventral rib-bearers. These are closely associated with the centra and anterior basapophyseal muscles.

The subcostal portion of the *subvertebralis* is thick, extending well below the level of the ribs and centra. The myomeres are here composed of two layers: the more ventral fibers run anterolaterally to become continuous with the *o. internus* distally, the dorsal fibers proceed posterolaterally, blending with the *o. e. profundus* distal to the ribs.

Excepting those associated with the second cervical (T1), spinal nerves exit intravertebrally through foramina in the wall of the neural arch. The nerves are situated dorsal to the posterior flexures in the trunk, but then extend to the ventral surface of the *subvertebralis*. Ventrally, each nerve lies next to the posterior edge of a myoseptum between the *transversus* and *o. internus* within the lateral abdominal wall.

Lateral abdominal musculature (see Figs. 37 and 38).- The lateral abdominal musculature is of typical larval aspect, being relatively thick and composed of all layers. The *o. e. superficialis* is applied against the lateral body wall, forming the external unit in this area. Ventrally it overlaps the *rectus abdominis*, but is not in contact with the epaxial myomeres dorsally. The *o. e. superficialis* is divided transversely by myocommata, between which the muscle fibers extend posteroventrally. Just below the horizontal septum, beneath the epaxial musculature, is found a well-developed *rectus lateralis*, which is not covered by the *o. e. superficialis*. Deep to the *r. lateralis* and *o. e. superficialis* the fibers of the *o. e. profundus* extend posteroventrally between adjacent myocommata. Dorsally there is some overlap of the segments of this layer, such that each unit extends over its posterior neighbour to some extent. The *o. e. profundus* is continuous with the *subvertebralis* dorsally and abuts the *r. abdominis* ventrally.

The *o. internus* is deep to the *o. e. profundus*, its fibers running anteroventrally. It has the same relationship to the *subvertebralis* and *r. abdominis* as does the *o. e. profundus*. The internalmost layer of lateral abdominal musculature, the *transversus*, is composed of fibers extending anteroventrally at an angle slightly displaced from the vertical. Dorsally it underlaps the *subvertebralis* and is here divided by myocommata. For approximately its ventral one half the *transversus* is not segmented. It does not quite reach the *r. abdominis* ventrally. The latter is a simple, small unit of muscle fibers extending anteroposteriorly between myocommata. Externally this band overlaps the *o. e. profundus* to some extent, internally it is very narrow. The two halves of the *r. abdominis* do not meet midventrally, but are separated by a thin strip of connective tissue.

Ambystoma maculatum (Shaw 1802)

RANGE. Found in the Maritime Provinces of Canada, west through central Ontario, and then south to the Gulf Coast, but lacking from Florida (Anderson 1967b).

HABITAT. "Restricted to hardwood and mixed deciduous forest . . . that have temporary or semi-permanent ponds available for breeding." The species is often lacking if ponds are periodically inundated by rivers or if there are permanent fish populations. The larvae seem to be competitively excluded by larval *A. tigrinum* from ponds (Anderson 1967b, p. 51.2).

FOSSIL RECORD. Known from the Upper Pleistocene of Missouri (Holman 1963).

RELATIONSHIPS. Tihen (1958) classified this species as the type of the *A. maculatum* species group in the subgenus *Ambystoma* along with *A. jeffersonianum* (q.v.), *A. laterale*, *A. platineum*, *A. tremblayi*, *A. gracile*, and *A. macrodactylum*. The defining characters of the group were held to be as follows:

1. Elongate vertebrae.
2. Relatively long and narrow premaxillary spines.
3. Parasphenoid concave laterally and with alar expansions posteriorly.
4. Vomers lacking a postdentigerous process.
5. Distinct gap between vomerine and palatine tooth rows.
6. Second basibranchial tending to be transverse.

The *A. maculatum* group was considered derived with respect to *A. tigrinum* and its allies. However, the structure of the vertebrae and the configuration of the component parts of the trunk musculature are distinctly more primitive in the *A. maculatum* group (in that they more closely resemble the hynobiid state), whereas *A. tigrinum* is derived via paedomorphosis. As noted above, I recognize separation of the species *A. macrodactylum* and *A. gracile* into a separate species group.

REMARKS. This species is relatively long-bodied, as are other members of the group. There are usually 12 costal grooves, although variation on either side of this number is present. The trunk, although long, is relatively stout, the limbs rather small but robust. The tail is long, somewhat compressed and lacks a dorsal crest.

Epaxial musculature (see Fig. 39).- The *dorsalis trunci* differs somewhat from the condition of *A. jeffersonianum*. Anterior flexures do not extend as far forward, but are more similar to those of other species of *Ambystoma*. In dorsal view almost the entire medial portion of the anterior flexure is visible without displacement of the myomere laterally.

Hyperapophyseal muscles are well developed, but resemble the condition in *A. tigrinum* more than that of *A. jeffersonianum*, in that the septum of each is long and narrow, with muscle fibers radiating medially and laterally. As in *A. jeffersonianum*, posterior slips from the main body of each myomere are present throughout the posterior half of the column. Other species of *Ambystoma* tend to have these septa restricted to the posterior one third of the trunk. Each slip has a wide area of insertion on the neural arch, just anterior to the postzygapophysis. From this point it narrows as it extends anterolaterally to the site of origin on the myomere.

The superficial fibers of the main body of the myomere extend anteroventrally, in contrast to the primarily anteroposterior alignment in *A. jeffersonianum*. The deeper fibers also exhibit this anteroventral orientation. The mass of muscle fibers contained in the myomere is proportionally less than in *A. tigrinum*.

Hypaxial musculature (see Fig. 39).- The *subvertebralis* differs from that of *A. jeffersonianum* in several minor aspects, although the two species are quite similar and retain the typical ambystomatid pattern. Midcentrally there is a strip along which the two halves of the *subvertebralis* do not meet. Anterior basapophyseal muscles are, correspondingly, narrower than in *A. jeffersonianum*. However, there are prominent anterior basapophyses on the lateral edges of the cotyles in the posterior region of the trunk. Basapophyseal muscles insert onto these projections. The atlas and at least the second cervical have posterior basapophyses, correlating with the differing structure of the myomeres immediately postcranially.

In the main part of each myomere, beneath the ribs, the superficial layer of muscle fibers aligns anterolaterally. Medial to this layer a ventral layer of fibers runs anteroposteriorly. The presence of these fibers causes the myomeres to seem simpler in superficial ventral view. Upon their removal, the short transverse process flexure is seen. A long, relatively deep septum extends posteriorly from it. This septum also has a medially extending, horizontal component. Dorsal to the superficial layer, fibers proceed posterolaterally, being continuous with the *o. e. profundus* distally. The myomeres of the *subvertebralis* drop anteroventrally from between adjacent ribs.

Excepting those associated with T1, spinal nerves exit intravertebrally, passing posterolaterally above the transverse process flexures. They are exposed to the peritoneal cavity at a level just distal to the ends of the transverse processes. From here they pass along the ventral surface of the myomeres until they disappear between the *transversus* and *o. e. profundus*.

Lateral abdominal musculature (see Fig. 39).- The lateral abdominal musculature is so similar to that of *A. jeffersonianum* as to require no description. That of *A. jeffersonianum* is described below.

Ambystoma jeffersonianum (Green 1827)

RANGE. Found south of the Great Lakes, "from southern Indiana and central Kentucky northeastward through most of Ohio to the southern half of New York, southern Vermont, western Massachusetts, northwestern New Jersey, and south through the ridge and valley province of Virginia to the New River in Virginia and West Virginia" (Uzzell 1967, p. 47.1).

HABITAT. "Mixed and deciduous woods with swamps, pools, and slow streams. Often extremely abundant on riverflats, where they hide by day beneath old logs, bark, or other surface cover" (Bishop 1943, p. 134). Larvae are of the pond type.

FOSSIL RECORD. None known.

RELATIONSHIPS. Tihen (1958) included this species in the *A. maculatum* group, the relationships of which are discussed under *A. maculatum* and *A. macrodactylum* above.

REMARKS. The trunk is long, but stout, with an elongate, laterally compressed tail. There are 12 costal grooves generally, and the limbs are robust with very long toes.

Epaxial musculature (see Fig. 40).- The epaxial musculature differs somewhat from that of other ambystomatids, including *A. maculatum*. Anterior flexures extend forward to a greater degree than in the species of *Ambystoma* described below. Each flexure is long and narrow, overlapping its anterior serial homologue for half the latter's length. The main body of each myomere rises posterodorsally from between adjacent ribs. This portion is of relatively smaller mass than in other ambystomatids and is laterally compressed. A long, relatively thin hyperapophyseal muscle underlies each anterior flexure. The septum of this muscle is long, taking up about half of its total length.

The superficial fibers of the main body of each myomere extend anteroposteriorly rather than anterolaterally (compare *A. tigrinum*). Posterior septal slips from each myomere are found in the rear half of the trunk. These run posteromedially from the main mass of the myomere to insert on the dorsal surface of the postzygapophysis of the next posterior vertebra. A distinct horizontal septum, marked by a superficial lateral vein, divides the *dorsalis trunci* from the hypaxial musculature.

Hypaxial musculature (see Fig. 40).- Anterior basapophyseal muscles are thick and wide, extending medially over the ventral surfaces of the centra. Intercentrally, small diamond-shaped areas are not covered by the *subvertebralis*. In this respect, and in the lack of anterior basapophyses for the insertions of the basapophyseal muscles, *A. jeffersonianum* resembles hynobiids. The transverse process flexures are relatively short and the main body of each myomere descends anteroventrally from between adjacent ribs. Spinal nerves exit intravertebrally, excepting those in association with T1, with their pathways laterally being as in *A. maculatum*. Ventrally the nerves disappear into the *rectus abdominis profundus*.

Lateral abdominal musculature (see Figs. 26 and 40).- The lateral abdominal musculature recalls that of hynobiids. The *o. e. superficialis* is the lateral, most external band. It spans the area between the *dorsalis trunci* and the *rectus abdominis*, overlapping each slightly. The *o. e. superficialis* is segmented, with the muscle fibers extending posteroventrally between the myocommata. Deep to this the *o. e. profundus* is found. It is a direct, ventral continuation of the intercostal muscles with fibers extending posteroventrally, but at a lesser angle than those of the *o. e. superficialis*. Ventrally, the fibers of the *o. e. profundus* overlap the *r. a. superficialis* in the posterior portion of each myomere.

Beneath the *o. e. profundus* is a very thin layer, also a continuation of the *subvertebralis*. This layer, although not extending to the *rectus abdominis*, is the *o. internus*, its fibers extending anteroventrally between the myocommata. The presence of a partially developed *o. internus* is presumably a foetal trait. Internally, next to the peritoneum, is found the *transversus*. Moving successively more ventrally, the external surface of the *transversus* lies against the *subvertebralis*, *o. internus*, *o. e. profundus*, *r. a. profundus*, and *r. a. superficialis*. Myosepta do not extend completely ventrally and the distal two thirds of the *transversus* is not segmented. The fibers extend anteroventrally.

The *rectus abdominis* is divided into two parts. The most exterior, *r. a. superficialis*, is segmented by myocommata that are continuations of those dividing the layers of lateral abdominal musculature discussed above. Its fibers run anteroposteriorly. The *r. a. profundus* is located between the *transversus* and the lateral part of the *r. a. superficialis*. The former unit extends freely between the hyobranchium and pelvic girdle, as in the species of Hynobius described above. Muscle fibers extend between the myocommata so as to produce a spiral unit of musculature. The condition of the *r. a. profundus*, shared with some hynobiids, *A. maculatum*, plethodontids, and some newts, is presumably a primitive feature.

Ambystoma opacum (Gravenhorst 1807)

RANGE. "From New Hampshire and central Massachusetts southward to northern Florida, westward through southeastern New York to the region of Lake Michigan and southward through the Mississippi basin to eastern Oklahoma and eastern Texas" (Anderson 1967a, p. 46.1).

HABITAT. Found in sandy and low-lying areas near streams and ponds. Better adapted to dry conditions than most other *Ambystoma*, and the only species of the family to deposit eggs on dry land in nests guarded by the female (Bishop 1943).

FOSSIL RECORD. None known.

RELATIONSHIPS. Tihen (1958) grouped *A. opacum* and *A. talpoideum* in the *A. opacum* species group, subgenus *Ambystoma*. Krogh and Tanner (1972) suggested that *A. talpoideum* was more closely related to the *A. maculatum* group than to *A. opacum*, but study of their data does not support their conclusions. Osteologically (Tihen 1958) and as concerns the trunk musculature, Tihen's (1958) grouping of these two species is corroborated. The characters used by Krogh and Tanner (1972) derive exclusively from the hyobranchial apparatus and many of these are subtle ratios. Study of the hyobranchium and of their descriptions does not support their suggested relations, which are, seemingly, an artifact of simplistic cluster analysis and the absence of interpretation. My studies indicate that *A. talpoideum* and *A. opacum* are derivable from a structural ancestor represented by *A. maculatum* or *A. jeffersonianum*, as was suggested by Tihen (1958).

REMARKS. The trunk is relatively stout, but less so than in *A. talpoideum*. There are generally 11 costal grooves, and the tail is very short.

Epaxial musculature (see Fig. 41).- Although differing in proportions, the *dorsalis trunci* is developed as in *A. talpoideum*. In dorsal view the medial part of each anterior flexure is hidden. When the myomeres are displaced laterally, the total extent can be seen. However, the anterior flexures are short and the medial portions narrow. In contrast to *A. talpoideum*, the main body of each myomere does not extend laterally beyond the ribs. From between each pair of ribs a myomere rises dorsally and posteriorly to overlap the myomere behind. The direction of the fibers in the epaxial myomeres is as in other species of *Ambystoma*. The posterior septum from the myomeres appears to be lacking throughout the column.

Hypaxial musculature (see Fig. 41).- Although of the same basic pattern, the *subvertebralis* is not notably similar in *A. opacum* and *A. talpoideum*. A median strip is not covered by musculature, leaving the ventral borders of the centra open to the peritoneal cavity. The myomeres in association with the atlas and second cervical have medial slips extending anteriorly to insert on the posterior basapophyses of these two vertebrae. The second trunk vertebra lacks basapophyses and anterior basapophyses are present on all remaining trunk vertebrae up to the sacral region. Associated anterior basapophyseal muscles are present and conformable to those found in *A. talpoideum*.

The transverse process flexures are longer than in *A. talpoideum*, with an elongate posterior septum. In this regard *A. opacum* is similar to other species of *Ambystoma*. The differing relative lengths in the two species of the *A. opacum* group may, in some way, be correlated with the burrowing habits of *A. talpoideum*. Excepting its deposition of eggs on land, *A. opacum* is more typically ambystomatid in its natural history. The remainder of the *subvertebralis* is developed as in *A. talpoideum*, and the relationships of the spinal nerves to the vertebrae and myomeres is conformable in the two species (see below).

Lateral abdominal musculature (see Fig. 41).- The lateral abdominal musculature of the two species of the *A. opacum* group is very similar and described under *A. talpoideum* below.

Ambystoma talpoideum (Holbrook 1838)

RANGE. Found on the coastal plains of South Carolina, Georgia, Florida, Alabama, Mississippi, Texas, and northwards along the Mississippi River and its eastern drainages (Bishop 1943).

HABITAT. This is a burrowing species, tending to be found in areas of sandy soil, but rarely in damp areas of leaf litter and rotting wood. Breeding occurs in ponds and other standing water (Bishop 1943).

FOSSIL RECORD. None known.

RELATIONSHIPS. A member of the *A. opacum* species group of Tihen (1958), the relationships of which are discussed above under *A. opacum*.

REMARKS. The trunk is stout and short in comparison to other ambystomatids. There are only 10 costal grooves and the tail is very short and rounded in cross-section.

Epaxial musculature (see Fig. 42).- In dorsal view the more medial parts of the anterior flexures are hidden, the myomeres appearing to sweep posteriorly from the midline. However, if the epaxial musculature is displaced laterally, the typical pattern of the ambystomatid anterior flexure is seen. In comparison to *A. tigrinum*, the anterior flexures are proportionally smaller with respect to the main body of the myomere. Positional relationships with the neural arches of adjacent vertebrae are as in *A. tigrinum*. Deep to each flexure is a small hyperapophyseal muscle. Based on topographic relationships it is homologous to the muscle of the same name in other ambystomatids, but appears to lack a septum anteriorly (compare *A. tigrinum*).

The main body of each myomere rises posterodorsally from between adjacent ribs. The more posterior trunk myomeres send a large septal projection posteromedially to attach to the posterior zygapophysis of the vertebra behind the two that the myomere spans. The main body extends further laterally beyond the ribs than is the case in either *A. tigrinum* or *A. opacum*.

Hypaxial musculature (see Fig. 42).- In essentials the *subvertebralis* is as in other species of *Ambystoma*. The most superficial, ventral layer of each myomere covers the basic folding of the myosepta. Medially these superficial fibers extend anteromedially; lateral to this they align anteroposteriorly; furthest laterally they extend anterolaterally. The *subvertebralis* leaves a narrow median strip along which the vertebral column is exposed to the peritoneum. Above the thin superficial layer the pattern of fibers and septa is relatively complexly folded.

A narrow basapophyseal muscle extends on either side of each centrum, originating along the lateral surface. These muscles insert on the lateral edge of each anterior cotyle, at which point in the posterior part of the column are developed small anterior basapophyses.

Anteriorly, including the atlas, second cervical (T1), and (often) the second trunk vertebra, are developed posterior basapophyses. The hypaxial musculature in association with these structures differs significantly from that in the posterior region of the trunk. A medial slip extends anteriorly from the second myomere to insert on each of the posterior basapophyses of the atlas. A similar slip extends anteriorly from each of the third myomeres to the second cervical.

Similar posterior basapophyseal slips are found in hynobiids (e.g., *H. retardatus*), but are lacking in both larval and adult *A. tigrinum*, being represented by very small, anteriorly extending septa. Such slips are present in adult *A. gracile*, but lacking from the larvae, indicating that the condition in *A. tigrinum* has been modified via paedomorphosis. These observations corroborate the suggestion that the *A. opacum*, *A. maculatum*, *A. macrodactylum*, and *A. cingulatum* species groups preserve the primitive pattern of axial musculature and vertebral structure for ambystomatids, whereas the other ambystomatine species groups and the dicamptodontines are modified. Based on cranial and vertebral structure, Tihen (1958) suggested that *A. tigrinum* and its allies represented the primitive species of *Ambystoma*. However, the above suggestion and mosaic evolution seem to better accord with the observations (see Conclusions).

Relative to that of *A. tigrinum* the transverse process flexure is quite short, with a very small posteriorly extending septum. Anteromedially each myomere sends forward a short, broad horizontal septum, which extends under the transverse process flexure of the next anterior myomere. Longitudinal fibers arise on the dorsal and ventral surfaces of this septum and extend to the transverse process flexure. Lateral to this the main portion of each myomere drops anteroventrally from between adjacent ribs, in which region the *subvertebralis* is very thick.

Excepting those associated with T1, spinal nerves exit intravertebrally, passing posterolaterally until each reaches the peritoneal surface of its myomere at a level just distal to the rib-bearers. From here they proceed laterally and ventrally to disappear between the *transversus* and *o. internus*. In the lateral abdominal musculature each nerve is found immediately posterior to a myocomma.

Lateral abdominal musculature (see Figs. 26 and 42).- Ventral to the *subvertebralis*, the abdominal musculature is divided into three layers, each of which is segmented by myocommata extending down from the *dorsalis trunci*. The most superficial *o. e. superficialis* extends between the *dorsalis trunci* and the *rectus abdominis superficialis*, both of which it overlaps slightly. The fibers of this layer are aligned posteroventrally at an angle just slightly displaced from the vertical.

Inside this layer the *o. e. profundus* is a direct continuation of the *subvertebralis*, passing ventrally to grade with the *r. a. profundus*. The *o. e. profundus* is thin, with the fibers running posteroventrally at an angle little displaced from the horizontal. This orientation, and its position next to the *o. e. superficialis*, indicate this unit to be the *o. e. profundus* rather than the *o. internus*. The *subvertebralis* extends a short distance ventrally between the *transversus* and *o. e. profundus*, this part being presumably the homologue of the *o. internus* (compare *A. jeffersonianum* and *A. tigrinum*). The internal *transversus* underlaps the *subvertebralis* slightly, is applied against the inner surface of the *o. e. profundus*, passes deep to the *r. a. profundus*, and partially extends onto the peritoneal surface of the *r. a. superficialis*. The *transversus* is segmented by myocommata for most of its length.

The ventral *rectus abdominis* is separated into two parts: the *r. a. profundus* and the *r. a. superficialis*. The latter forms the external band of longitudinal muscle seen in ventral view in a skinned specimen. Its medial part is thickest, abutting laterally against the *r. a. profundus*. Its ventrolateral portion is thin, extending dorsolaterally exterior to the *r. a. profundus*. The deep part of the *rectus abdominis* is complex, appearing to be a ventral continuation of the *o. e. profundus*, which is folded back over itself. Its internal layer has fibers extending anteromedially between myocommata, whereas the more external part has fibers running anteroposteriorly.

Ambystoma cingulatum Cope 1867

RANGE. Found from South Carolina along the coastal plain through Georgia and into northern Florida. Also west across northern Florida along the Gulf Coastal Plain to easternmost Mississippi (Martof 1968).

HABITAT. "Flatwoods dominated chiefly by slash pine . . . and wire grass . . . . Adults are often found beneath logs near shallow ponds or swamps. These aquatic sites are the breeding and larval habitats" (Martof 1968, p. 57.1).

FOSSIL RECORD. None known.

RELATIONSHIPS. Tihen (1958) grouped *A. cingulatum* with *A. mabeei*, *A. schmidti*, *A. texanum*, and *A. annulatum* in the subgenus *Linguaelapsus*, which he considered to have been "derived at a relatively early date from the *maculatum-opacum* group precursor stock" (p. 46). *Linguaelapsus* was distinguished by the following features:

1. Long, narrow premaxillary spines (closely appressed above the dental shelf in *A. cingulatum*).
2. Several rows of teeth on all tooth-bearing elements (except in *A. mabeei*).
3. No teeth on palatine portion of vomer (except in *A. mabeei*).
4. No lingual flange of bone on dentary.
5. Annular otoglossal cartilage lacking.
6. 13 to 15 costal grooves, body elongate with respect to the subgenus *Ambystoma*.
7. Vomer with postdentigerous process, as in the *A. tigrinum* species group.

A. cingulatum and *A. texanum* are very similar, but the position of *A. mabeei* within the subgenus *Linguaelapsus* is problematical (Tihen 1958).

Tihen (1958) considered *Linguaelapsus* to have primitive and/or neotenic features (e.g., lack of an annular otoglossal, lack of lingual flanges on the dentary, and a posteriorly expanded parasphenoid). He concluded, however, that these were to be interpreted as owing to partial foetalization rather than to the retention of primitive characters. *Linguaelapsus* was believed to have been derived from the "*maculatum-opacum* group precursor stock" after the latter had split from the *A. tigrinum* stock. In light of my findings, however, it is more likely that in the *A. cingulatum* group the features noted by Tihen are owing to retention of primitive features. I agree that it is derived from *A. maculatum* stock, but argue that the latter is primitive with respect to *A. tigrinum* and its allies (see Conclusions). Further, I do not believe it necessary to continue recognition of a subgenus *Linguaelapsus*, which may be referred to as the *A. cingulatum* species group.

REMARKS. This is a relatively small species (3.5 inches being an average adult size, see Bishop 1943) of *Ambystoma*, with an elongate, relatively robust trunk and 13 or 14 costal grooves. The limbs are small for an ambystomatid and when appressed leave one or two intercostal folds between the toes. The tail is long, oval in cross-section, and but slightly compressed laterally. The teeth are in rows on all tooth-bearing elements and their apices are broadly oval and spade-like.

Owing to the condition of the anatomical specimens at my disposal it has not proven possible to elucidate sufficient detail of the trunk musculature to make descriptions or drawings of this species useful. However, it can be said that the structure is conformable to that of the *A. maculatum* group and that it tends to confirm an hypothesis of derivation from that group.

Ambystoma tigrinum (Green 1825)

RANGE. Very widespread over the North American continent, excepting mountainous, cold, or very dry areas (see Gehlbach 1967 for range map).

HABITAT. Found in areas "with substrates suitable for burrowing" (Gehlbach 1967, p. 52.1) and with standing water for breeding.

FOSSIL RECORD. Known from the upper Pliocene and through all stages of the Pleistocene in Arizona, Florida, Georgia, Kansas, and Texas (Gehlbach 1967). Tihen (1942) reported a large number of remains of neotenic *A. tigrinum* from the latest Pleistocene of Kansas. *A. kansense*, from the upper Pliocene of Kansas, is very close to *A. tigrinum* and placed in the *A. tigrinum* species group (Tihen 1955, 1958).

RELATIONSHIPS. Tihen (1958) recognized two species groups for the *A. mexicanum* and *A. tigrinum* complexes, plus a separate subgenus *Bathysiredon* for *A. dumerilli*. More recent work by Brandon (1970a,b, 1972, 1976, 1977) indicates very close relationship between the species of these groups. Although Tihen's (1958) groupings can certainly be justified, I prefer to recognize only a single species group, the *A. tigrinum* group, including Tihen's (1958) *A. tigrinum* group, *A. mexicanum* group, and subgenus *Bathysiredon*. This complex includes the most derived species of *Ambystoma*, characterized by paedomorphosis. There is little doubt as to the apomorphic nature of these species, based on ontogenetic considerations and on in-group and ex-group comparisons. As demonstrated below, Tihen's (1958) phylogenetic hypothesis for *Ambystoma* cannot be accepted.

REMARKS. In well-fed specimens the trunk is very stout and robust, recalling the larval form of other *Ambystoma*. There are generally 12 costal grooves and the body is roughly lens-shaped between the limb girdles. The limbs are powerful, but short.

Epaxial musculature (see Figs. 44 and 45).- The *dorsalis trunci* is segmented in a manner conformable to the pattern in hynobiids and other ambystomatids. The anterior flexure extends about one half of the distance along the first vertebra of the pair spanned by its myomere. The main body of the myomere is swept somewhat further posteriorly than is the case in the Hynobiidae. This may, in some way, correlate with the presence of more divergent rib-bearers in this species than in either hynobiids or the more primitive ambystomatines described above.

Beneath each anterior flexure, and inserting on the posterior edge of a hyperapophysis, is a small hyperapophyseal muscle. These are paired, two originating on the neural arch of each vertebra and inserting on the hyperapophysis of the next anterior vertebra by means of septa. Muscle fibers fan medially and laterally from each septum. The homologous muscles of hynobiids are not differentiated into such discrete units. In these the septum proceeding anteriorly and ventrally from the anterior flexure attaches to the neural arch of the next anterior vertebra. This ventral attachment is lacking from *A. tigrinum* and the other ambystomatids here described, resulting in the differentiation of a free hyperapophyseal muscle.

In the posterior third of the trunk a septum extends posteromedially from the main body of each myomere to attach to the dorsal surface of the postzygapophysis of the vertebra following the pair with which its myomere is associated. This septal slip is similar to that described in some hynobiids, but its insertion is further medial in this species of *Ambystoma*. In the main body of each myomere, lateral to the anterior flexure, the more superficial fibers align anterolaterally. Deep to these, the muscle strands extend anteroposteriorly.

Hypaxial musculature (see Fig. 44).- The hypaxial musculature is conformable to that of the species of *Ambystoma* discussed above, but differs in proportions. The *subvertebralis* fails to cover a median strip along the column. A thin sheet of muscle covers the main body of the myomeres, the fibers partly overlapping the more complex medial parts that are dorsal to it. Basapophyseal muscles are relatively narrow, but low robust anterior basapophyses are present for their insertions in larger adults. The posterior flexure from each transverse process is relatively short and wide, with an elongate, posteriorly projecting septum on each. A short, but prominent anterior flexure projects from below the articulation between the rib and its transverse process. From the anterior flexure, the main body of the myomere proceeds posterolaterally at a pronounced angle. Each myomere overlaps the posterior part of its anterior neighbour, and extends posterolaterally to grade into the *obliquus internus*.

Spinal nerve exits are intravertebral, excepting for T1, which lacks foramina. The nerves pass posterolaterally dorsal to the transverse process flexures, until they reach the ventral surface of each myomere. Each nerve then extends along the peritoneal surface until covered by the *transversus*. Laterally and ventrally the nerve is found between the *transversus* and *o. internus*, just posterior to the myocomma of each segment. It finally disappears into the *rectus abdominis*.

Lateral abdominal musculature (see Figs. 44 and 45.)- *A. tigrinum* has four layers in the lateral body wall and a simple ventral *rectus abdominis*. This condition is a secondary, paedomorphic development. The *obliquus externus superficialis* is as in the Hynobiidae, but there is individual variation in its dorsal extent. In some, it does not overlap the epaxial musculature, but is bound to the *o. e. profundus* so as to leave a gap dorsally beneath the epaxial portion of the myomere. More commonly, however, it overlaps the *dorsalis trunci* for a very short distance. The muscle fibers of the *o. e. superficialis* extend posteroventrally at a high angle and are segmented by myocommata. The deeper *o. e. profundus* grades dorsally with the *subvertebralis* and ventrally with the *rectus abdominis*. Its fibers extend anteroposteriorly just ventral of the *dorsalis trunci*, but run posteroventrally throughout the remainder of the unit.

The *o. internus* also grades with the *subvertebralis*, but not with the *r. abdominis*. Its muscle fibers extend anteroventrally, but at a lesser angle than those in the *transversus*. The internalmost *transversus* underlaps the *subvertebralis* dorsally and the *rectus abdominis* ventrally. Muscle fibers proceed anteroventrally and are not divided by myocommata in the distal half of the *transversus*. The relatively thick *rectus abdominis* is a single, simple ventromedial band of muscle fibers extending anteroposteriorly. This is a larval characteristic.

Larvae (see Fig. 43).- The trunk of unmetamorphosed specimens of *A. tigrinum* is very deep and somewhat laterally compressed. However, this distinction from metamorphosed individuals is owing to the larger size of the internal organs (especially of the digestive tract) and not to a larger mass of musculature. Because of the differing demands of terrestrial locomotion, adults have a greater mass of axial musculature. In larvae and neotenes the locomotory function is concentrated in the tail, the trunk remaining relatively immobile during swimming. On land, adults use the bending of the trunk as an important aid in walking (Roos 1964, Edwards 1977) and, in aquatic locomotion, the whole body is thrown into curves.

Epaxial musculature of the larva is concentrated dorsolateral to the vertebral column. The myomeres do not contact each other middorsally, and there is a lesser amount of musculature in the *dorsalis trunci* than in the adult. Anterior flexures extend anteriorly a somewhat shorter distance than in adults. In the posterior part of the trunk myomeres exhibit posterior overlap to a greater degree than in the anterior part. A posterior septal slip from the myomere extends posteromedially to insert on the dorsal surface of the postzygapophysis of the vertebra behind the pair spanned by the myomere.

The *subvertebralis* possesses the same pattern as in adult specimens, but there is a lesser mass of musculature present. Anterior basapophyseal muscles are small and thin, and basapophyses are, therefore, absent in larvae. The posterior flexure from each transverse process is developed to about the same extent as in the metamorphosed adult, although the septum projecting posteriorly from it is relatively much shorter. The main body of each myomere is thinner in the larvae, but the directions of the muscle fibers are conformable to the condition in terrestrial specimens. Spinal nerves share the same relationship to vertebrae and musculature as in the adult.

The relationships and orientations of the muscle fibers of the lateral abdominal musculature are the same in the two ontogenetic phases of the tiger salamander. The abdominal wall of the larva, however, is much thinner and the two halves of the *rectus abdominis* are distinctly separated by a band of fascia.

v) Family Proteidae Hogg 1838

Necturus maculosus Rafinesque 1820

RANGE. "The Mississippi River system from the Arkansas River and northern Alabama northward; the Great Lakes and St. Lawrence and their tributaries in Manitoba, Ontario, and Quebec; Lake George and Lake Champlain, Mohawk River and Barge Canal, middle Hudson . . . , Susquehanna River, Delaware River . . . , Connecticut and Farmington rivers in New England (introduced)" (Bishop 1943, p. 40).

HABITAT. Completely aquatic "in the clear waters of lakes and streams, but [also] occurs in muddy and weed-choked bays and coves, and in canals and drainage ditches" (Bishop 1943, p. 40).

FOSSIL RECORD. *Comonecturoides*, known from a single femur from the Upper Jurassic of Wyoming, has been referred to the "Necturidae" by Hecht and Estes (1960), but its relationship to *Necturus* is problematical. Vertebrae of a new species of *Necturus* from the upper Paleocene of southern Saskatchewan are known (see Fig. 13, also Naylor 1978b). Romer (1966) notes *Necturus* as questionably present in the Oligocene of North America, but the source of this referral is unknown to me. A vomer possibly of *Necturus* from the lower Miocene Gering Formation was collected by the University of Nebraska, but lost before it could be described (Estes, pers. comm.). Lynch (1965) reported vertebrae of *Necturus* in the Pleistocene of Florida, outside the present range of the genus.

RELATIONSHIPS. Hecht (1958) reviewed the nomenclatorial history of *Necturus* and its included species. He divided the genus into three species groups: the *N. punctatus* group (with two subspecies of *N. punctatus*), the *N. lewisi* group (*N. lewisi* and two subspecies of *N. beyeri*), and the *N. maculosus* group (monotypic with three subspecies). Brode (1970), however, recognizes only two species, *N. maculosus* and *N. punctatus*, each with three subspecies.

In spite of the arguments of Hecht (1957) and Hecht and Edwards (1976), there is no good reason to consider *Necturus* as merely convergent upon *Proteus*. Larsen and Guthrie (1974), Kezer et al. (1965), and Brandon (1969) have provided convincing evidence for close relationship of the two proteid genera. Additional evidence and a critique of the contentions of Hecht and Edwards (1976) are considered below (also Naylor 1978b). The two genera are here considered to be closely related and monophyletic. Familial relationships are discussed in the Conclusions.

REMARKS. The trunk is elongate, somewhat dorsoventrally compressed, and stout, with 15 costal grooves usually present. The limbs are small but well developed and active in locomotion over the substrate. The tail is short, laterally compressed, and high. The trunk musculature is simplified and distinctive. Auffenberg (1959) has described the epaxial musculature of *Necturus*, concluding (incorrectly) that it shows a primitive condition. Certain of his observations differ from mine and corrections are given below.

Epaxial musculature (see Fig. 46).- Auffenberg (1959, p. 263) stated that in comparison with *Siren* and *Amphiuma*, "*Necturus* is decidedly the most primitive in its epaxial fiber tracts," and (p. 253) that "in regard to the deeper tracts *Necturus* is most primitive." These interpretations are owing to evident confusion over primitive and simple features, and to lack of information as to the conditions in other urodeles. Complexity is not necessarily synonymous with derived character states, especially in salamanders. It is evident that *Necturus* is, in fact, very derived as regards its trunk musculature, almost certainly having evolved from an opisthocoelous ancestor. The pattern of its trunk musculature differs greatly from the basic, presumably primitive, condition of hynobiids and ambystomatids (q.v.).

The epaxial myomeres are somewhat simplified, but still of basic urodelan plan. Anterior flexures are produced a short distance forward and are quite narrow. The full extent is evident only when the *dorsalis trunci* is displaced laterally. The main body of the myomere rises gently posterodorsally from between adjacent ribs. Auffenberg's (1959, p. 257) brief description of the attachments of the myosepta to the vertebrae is incorrect. The septum does attach "to the posterior edge of the neural arch [= hyperapophysis] of one vertebra," but the connection does not then extend "posteriorly to the succeeding vertebra along the dorsal surface of its transverse process." Rather, the septum extends along the lateral edge of the hyperapophysis of the first vertebra, then along the edge of the postzygapophysis to the transverse process of the same vertebra. It extends along the posterodorsal edge of the transverse process and rib distally. This is the basic situation throughout the Caudata.

Unlike the condition in the anguilliform salamanders, *Amphiuma* and *Siren*, but as in *Cryptobranchus*, there is relatively little musculature located dorsal to the vertebral column. There is an increased mass of musculature relative to normally metamorphosing salamanders, but this is positioned dorsolateral and lateral to the column.

A thin septum is located deep to each anterior flexure, extending from the hyperapophysis to which it attaches, posteriorly over the surface of the neural arch of the succeeding vertebra. Muscle fibers extend posteromedially and posterolaterally from each septum, producing the hyperapophyseal muscles. In addition to this system, there is developed a zygapophyseal septal system. Each of these septa arises on the anterior, dorsal surface of a posterior zygapophysis just below the attachment of the hyperapophysis to the neural arch. The septum extends anterolaterally into the myomere from this point. Medially, fibers extend anteromedially to the hyperapophyseal septum. Laterally, the fibers run anterolaterally and anteriorly to the next anterior vertebra and its associated myoseptum. The zygapophyseal septa and their associated muscle fibers presumably serve to concentrate force on the posterior portion of each vertebra.

The fibers of the main body of each myomere extend anteroposteriorly, both superficially and deep. The most posterior myomeres, anterior to the sacrum, have a deep posterior flexure. This flexure arises from the posteromedial surface of the main body of the myomere and extends posteromedially to insert on the anterolateral edge of the hyperapophysis of the vertebra behind the pair spanned by its myomere. These flexures are broad near their origins from the myomeres and narrow to the points of insertion.

Auffenberg (1959, pp. 258-259) describes certain of the "myoseptal-vertebral" muscle fibers as follows: "The fibers run from the postero-dorsal surface of the transverse process of one vertebra posteriorly to the anterior surface of the succeeding septum, and from the posterior surface of this septum to the antero-dorsal surface of the succeeding transverse process. Thus fibers run anteriorly and posteriorly to each septum from the preceding and succeeding transverse processes." For this system to be true, there would have to be fibers crisscrossing in each myomere. The utility of such a system is obscure and, indeed, I find no such network in specimens available to me. Instead, the muscle fibers extend anteroposteriorly in this region parallel to one another.

Hypaxial musculature (see Fig. 46).- The *subvertebralis* resembles that of *Salamandra* (q.v.), but is derivable from a system similar to that of some plethodontids as well. This genus differs from paedogenic salamanders of other families in the simple development and relatively small mass of the *subvertebralis*, but closely resembles *Proteus*. In some specimens the ribs are exposed ventrally to the peritoneal cavity. More often, however, they are covered, although to a limited degree, by musculature. In these cases the rib is covered by muscle fibers from the myomere situated behind it.

Except for a relatively short, broad posterior flexure extending back from each transverse process, each myomere is limited to the area between two adjacent vertebrae and the associated ribs. This posterior flap is remarkably similar to that of *Salamandra* and is undoubtedly homologous to the posterior flexure of plethodontids and, by extension, to the transverse process flexure of ambystomatids. The large posterior basapophyses of the extinct batrachosauroidids are of note in this regard, as they indicate the presence of similar posterior flexures, although modified to form posterior basapophyseal muscles. The most superficial, ventral muscle fibers extend anteroposteriorly in the area below the transverse processes, and anterolaterally beneath the ribs. This layer is thin, but blends laterally into the thick *obiquus internus*. Dorsal to this peritoneal layer, muscle fibers extend anteroposteriorly. Laterally and ventrally this group merges into the fibers of the *o. e. profundus*.

Except for those associated with the atlas, spinal nerves exit intervertebrally, a condition probably of secondary derivation. Small larval newts of at least some species (e.g., *Triturus vulgaris*) have intervertebral exits, although this is soon converted to the intravertebral condition. The nerves in *Necturus* pass posterolaterally through the *subvertebralis* to become exposed to the peritoneal cavity at a level just distal to the ends of the transverse processes. They are then covered internally by the *transversus*. More distally, the nerves are located between the *transversus* and *o. internus*, adjacent to the posterior edge of each myoseptum.

Lateral abdominal musculature (see Figs. 46 and 47).- Maurer (1892, 1911) described and figured the lateral abdominal musculature of *Menobranchus lateralis* (= *Necturus maculosus*). However, as certain of his observations differ from mine, redescription is necessary. The condition of the musculature conforms generally to that described by Mivart (1869, p. 453) and Walker (1970). An *obliquus externus superficialis* is present, but as an extremely thin unit formed of only a single layer of muscle fibers. Its delicate nature probably accounts for the failure of both Mivart (1869) and Walker (1970) to note its presence. The *o. e. superficialis* overlaps the epaxial musculature to a significant degree. From here the fibers extend posteroventrally at an angle somewhat displaced from the vertical and overlap the *rectus abdominis* ventrally (see also Maurer 1892, pl. V, fig. 9, and 1911, pl. II, fig. 6).

The *o. e. profundus* is a very thick layer, being a direct ventral continuation of the intercostal musculature. Its fibers extend posteroventrally and blend ventrally with the simple *r. abdominis*. Maurer (1911, pl. II, fig. 6) shows a small *rectus lateralis* external to the *o. e. profundus* and just below the *dorsalis trunci*. The validity (or usefulness) of distinguishing such a separate band is problematical, as its fibers are not separable from those of the *o. e. profundus*. There are, nevertheless, muscle fibers aligning anteroposteriorly in the area of the *r. lateralis* of other salamanders, labelled 'x' by Maurer (1911).

Deep to the *o. e. profundus* a layer of muscle fibers extends anteroventrally. This is the *o. internus*, also a direct continuation of the *subvertebralis*. The *rectus abdominis* is not set off from the other units of the lateral abdominal musculature. Ventrally the muscle fibers of the *o. e. profundus* and *o. internus* blend together and come to extend anteroposteriorly between myocommata; this is the *rectus abdominus*. Although Maurer (1892, p. 96, and 1911, pl. II, fig. 6) notes and figures a *rectus abdominis profundus*, I find no trace of this muscle in *Necturus*, nor do Mivart (1869) or Walker (1970) mention it. Walker (1970, p. 126) terms the *r. abdominis* of *Necturus* as "incipient". However, in other features of the trunk musculature this genus is highly apomorphic and comparison with larval and adult conditions in other families shows clearly the secondary nature of the simple proteid *rectus abdominis*. It is a reduced, paedomorphic condition.

The deepest layer of lateral abdominal musculature is the *transversus*, found next to the peritoneal cavity. This layer has fibers extending anteroventrally at an angle little displaced from the vertical. The *transversus* is applied against the ventral surface of the *subvertebralis*, underlapping the latter to a significant degree. Tough fascia extends medially from the dorsal edge of the *transversus* under the *subvertebralis*. The dorsal third of the *transversus* is segmented by myosepta continuous from the distal ends of the ribs. The remainder of the unit is free of this.

The lateral abdominal musculature of *Necturus* superficially resembles that of paedogenic salamanders of other families (*Cryptobranchus*, *Amphiuma*, and *Siren*) in being very massive. However, it differs significantly in detailed structure from these, while being similar to *Proteus* (q.v.).

Proteus anguinus Laurenti 1768

RANGE. The monotypic *Proteus* is known only from Yugoslavia and (perhaps) Austria (Thorn 1968).

HABITAT. Found only in the cool waters of underground lakes and streams in limestone caves, the species seems to prefer areas of weak current and muddy bottoms (Thorn 1968, p. 118). It is apparently to some extent a burrower in mud and sand (Steward 1969), as seems reasonable considering its structure. "Food . . . consist[s] largely of a local freshwater crustacean of the genus *Nyphargus*" (Steward 1969, p. 148). The species can be either ovoviviparous or oviparous.

FOSSIL RECORD. *Hylaeobatrachus* Dollo 1884, from the Lower Cretaceous of Belgium, may be related to *Proteus* (see Conclusions). The position of *Palaeoproteus* Herre 1935 from the Paleocene and Eocene of Europe remains uncertain. Herre (1935b) considered it to be a proteid, but Estes et al. (1967) suggested that it was a salamandrid. I consider it a member of the Batrachosauroididae (see Naylor 1978a, also below). *Orthophyia*, from the Miocene of Europe, is possibly related to *Proteus*, as suggested by Herre (1935b), Kuhn (1962), and Brame (1967). Brunner (1956) named a new species of *Proteus*, *P. bavaricus*, from a Pleistocene cave deposit of the Riss-Würm interglacial (but see Estes and Darevsky 1977). Estes and Darevsky (1977) named a new genus and species of proteid salamander from the Miocene of the Caucasus. *Mioproteus caucasicus* is known from trunk and caudal vertebrae, an atlas, parts of the hyobranchial skeleton, vomers, and dentaries.

This species shows resemblances to both *Necturus* and *Proteus* and may represent the genus *Orthophyia*, for which all material has been lost (see Estes and Darevsky 1977).

RELATIONSHIPS. *Proteus* is here considered to be closely related to *Necturus*, with which it forms a monotypic family. The reasons for this and the relationships of the Proteidae are discussed below in the Conclusions.

REMARKS. *Proteus* is an elongate, thin salamander recalling *Siren* in form. The trunk is long (ca. 25 costal grooves) and subcircular in cross-section. The tail is short and laterally compressed. The head is large, flattened, and spade-like, with enlarged, overhanging lips. The eyes are buried beneath the skin. In spite of attenuation, *Proteus* is similar to *Necturus* in overall form.

Epaxial musculature (see Fig. 48).- The two halves of the *dorsalis trunci* are distinctly separated by a middorsal band of adipose tissue, which extends ventrally to the tops of the neural arches. The myomeres resemble those of *Necturus*, but are somewhat modified. Anterior flexures are narrow, shortened, and simplified. The internal, anteromedially extending group of muscle fibers is lacking from each anterior flexure, but the anterolaterally extending group remains. Anterior flexures are well set off from their adjoining myomeres, with an area filled with a small, elongate unit of adipose tissue separating each main body from its anterior flexure. The main body of each myomere is wide and produced far anteriorly under its anterior neighbour. Muscle fibers in each extend anteroposteriorly, but with a definite anterolateral component. Modifications for the elongate body and anguilliform swimming are evident in the distinction between the anterior flexures and the main bodies, and in the steep posterodorsal rise of the main bodies, as opposed to the simple overlap of the myomeres seen in "normally" proportioned salamanders.

The deep posterior flexures described in *Necturus* are lacking from *Proteus*, possibly owing to the myomeres extending much further posteriorly in the latter. Likewise, the zygapophyseal septa and associated muscle fibers of *Necturus* appear absent in *Proteus*

Hypaxial musculature.- The *subvertebralis* is underlain by tough fascia, on which the *transversus* originates laterally. Medially a simple posterior flexure is developed in association with the subcentral keel. These are similar to those seen in *Necturus*, but in more intimate association with the centra. They are formed by a septal ribbon originating on the posterior cotyle of one vertebra and extending back to parallel the subcentral keel of the following vertebra. Muscle fibers fan from each septum, posteromedially to the subcentral keel, posterodorsally and posterolaterally onto the ventral lamella, and posterolaterally to a septum, which descends from the forward edge of the ventral lamella. The posterior flexures thus formed are more distinct from the main bodies of the myomeres than is the case in *Necturus*.

The myomeres do not extend anteriorly beyond the edges of the ventral lamellae, thereby producing a slight gap between adjacent myomeres, which is filled with adipose tissue. The posterior flexure and main body of each myomere form an L-shaped structure, with the flexure forming the backwardly projecting, short arm of the L and the main body forming the posterolaterally extending long arm. The main bodies are formed of two units of fibers, the ventralmost layer extending anterolaterally between myosepta and the more dorsal layer proceeding posterolaterally. Ribs are lacking on the trunk vertebrae and these layers blend completely with the *o. internus* and *o. e. profundus*, respectively.

Excepting those of the atlas, spinal nerves exit intervertebrally, passing through the *subvertebralis* until just before the *transversus* is reached. Here they are exposed for a short distance to the peritoneal cavity. In the lateral abdominal musculature they extend between the *transversus* and *o. internus*, each one just posterior to a myocomma.

Lateral abdominal musculature (see Fig. 48).- The lateral abdominal musculature is all but identical to that of *Necturus*. The *o. e. superficialis* is not distinct, but is a very thin unit, the fibers of which extend posteroventrally at much the same angle as those of the *o. e. profundus*. It is distinguishable from the *o. e. profundus* owing to overlap of the *rectus lateralis* dorsally. The latter muscle is thick and not clearly set off from the *o. e. profundus*.

The *o. e. profundus* is thick, its fibers extending posteroventrally between the myocommata. Both it and the *o. internus* are as described in *Necturus*. The *transversus* is also thick, but not divided by myocommata, although it is otherwise as in *Necturus*. According to Maurer (1892) the *transversus* originates, as in *Siren*, on tendons connecting the transverse processes of the vertebrae. This is not, strictly speaking, correct. Part of the *transversus* is attached to the ventral surface of each transverse process by fascia, but not as in *Siren*, in which the *transversus* attaches to the transverse processes over a very wide area and extends into the *subvertebralis* to do so. Although not segmented, the *transversus* of *Proteus* attaches to the myocommata of the *o. internus* dorsally.

The *o. e. profundus* and *o. internus* are formed such that there is overlap of each segment of the lateral abdominal musculature. This overlap is a continuation of the overlap of the myomeres of the *dorsalis trunci* and resembles the situation in *Siren*, which doubtless reflects convergence in long-bodied anguilliform or pro-anguilliform organisms. Ventrally the *o. e. profundus* and *o. internus* merge to form the simple, although relatively thick, *rectus abdominis*. The muscle fibers of this extend anteroposteriorly. Maurer (1892, 1911) describes a *rectus abdominis profundus* in *Proteus* that supposedly connects to the hyobranchium. Muscles from the *rectus abdominis* do extend onto the branchial arches, but there is no trace of a *r. a. profundus* in *Proteus*.

vi) Family Plethodontidae Gray 1850

a) Subfamily Plethodontinae Boulenger 1882

Tribe Plethodontini Wake 1966

Plethodon Tschudi 1838

RANGE. Especially common in the Appalachian Mountains, but ranges north into Canada, south into Florida, and to the Gulf of Mexico. Also found westward to Texas and almost to the region of the Great Plains. *P. neomexicanus* is found in the Jemez Mountains of New Mexico. The

West Coast species are found on Vancouver Island, southeastern British Columbia, and then down the coastal areas into northern California. There are isolated populations in Idaho and Montana (see Highton 1962, Stebbins 1962).

HABITAT. The members of this genus are secretive and totally terrestrial. Eggs are laid on land and brooded by the female. More details are given under the individual species below (see also Dunn 1926).

FOSSIL RECORD. *Plethodon* is first known from the latest Pleistocene of Florida (Holman 1958, 1959a,b), where it is represented by fossil vertebrae of the living species *P. glutinosus*. Tihen (1968, p. 114) claimed *Plethodon* probably appeared "before or during the Miocene," but to my knowledge this is not documented by fossil evidence.

RELATIONSHIPS. The genus has a disjunct distribution, one group found in eastern North America and the other on the West Coast. Dunn (1926) considered that *Plethodon* was derivable from no existing genus and that it was the most primitive member of a generic group also including *Ensatina*, *Hemidactylium*, *Aneides*, and *Batrachoseps*. Primitive features were held to include few costal grooves (correlated with a lower number of trunk vertebrae), a long vomerine tooth series, double premaxillae, and pale dorsal markings. Dunn also suggested that the most primitive species were those in the *P. glutinosus* group (also including *wehrlei*, *jordani*, *shermani*, *metcalfi*, and *yonahlossee*). The *P. cinereus* group (eastern small plethodons) was thought to be more derived, whereas the western plethodons were the most derived. Wake (1966) considered *P. yonahlossee* to be the most primitive of its genus.

Highton (1962, 1972) followed Dunn's division of *Plethodon* into three species groups. However, he considered the western and eastern small plethodons to be more primitive than the eastern large plethodons (Dunn's *P. glutinosus* group). Wake (1966) modified Dunn's generic grouping by removing *Hemidactylium* and *Batrachoseps* to other tribes, the Hemidactyliini and Bolitoglossini respectively.

My studies tend to provide support for the conclusions of Dunn (1926) and controvert the suggestions of Highton (1962, 1972) and Wake (1966). Arguments are presented below (see Conclusions), but a brief summary is given here. I consider *Hemidactylium* and *Batrachoseps* to be closely allied to *Plethodon* and to be classified in the Tribe Plethodontini (Dunn's *Plethodon* group). The aquatic larval stage of *Hemidactylium* is probably a secondary reversion, as suggested by Dunn and not controverted by any subsequent work. *Batrachoseps* cannot be closely related to the bolitoglossines as it lacks a free tongue. These reinterpretations necessitate renaming Wake's (1966) Hemidactyliini the Euryciini, as *Hemidactylium* is removed.

Within the genus *Plethodon*, Dunn's hypothesis of relationships is also to be upheld. Highton's (1962) primary criteria of morphocline polarity are the numbers of trunk vertebrae and patterns of coloration. The former can certainly be used to some extent in the elucidation of relationships. However, the use of patterns of coloration is, unfortunately, useless. Colour is extremely plastic, changing rapidly as ecological relationships and background colours change (e.g., Cott 1940, Thayer 1909). At least in salamanders of this genus, the colour patterns are undoubtedly serving a cryptic function, permitting no utility for phylogenetic reconstruction.

Based on the structure of the trunk musculature, structure of the vertebrae, and ex-group comparisons of these features, the eastern large plethodons are seen to be the most primitive members of the genus. The eastern small and western plethodons are derived with respect to this group, perhaps having evolved independently with no special relationship to each other. I also consider that *P. neomexicanus* should be placed in its own species group (see also Muizuno and MacGregor 1974), being perhaps derived from the eastern large plethodons. The four species groups of *Plethodon* may be referred to as the *P. glutinosus* group (Highton's eastern large plethodons), the *P. cinereus* group (eastern small plethodons), the *P. neomexicanus* group (monotypic), and the *P. vehiculum* group (western plethodons).

Plethodon jordani Blatchley 1901

RANGE. Found in "the Great Smoky Mountains in western North Carolina and eastern Tennessee" (Bishop 1943, p. 261).

HABITAT. "This species is abundant in and beneath old rotten, moss-covered logs and bark and, more rarely, beneath stones and slabs of rock" (Bishop 1943, p. 261). Eggs are lain on land and brooded by the female. According to Dunn (1926, p. 14) *P. jordani* is often fossorial in rotten wood.

FOSSIL RECORD. None known.

RELATIONSHIPS. A member of the *P. glutinosus* species group (eastern large plethodons of Highton 1962, 1972), considered by Highton to be derived, but in fact probably the most primitive species of *Plethodon*.

The genus *Plethodon* is most closely related to *Aneides* and *Ensatina*, but *Hemidactylium* and *Batrachoseps* are also allied. According to Highton (1962), *P. jordani* and *P. glutinosus* are very closely related.

REMARKS. *P. jordani* has a long, relatively narrow trunk with 15 or 16 costal grooves. The tail is long and robust, and subject to breakage at any point along its length. The trunk is very long for a non-neotenic species, this perhaps being one of the reasons for the development of functional opisthocoely in larger individuals (see Conclusions). The limbs are quite small and short, with two or three costal grooves remaining between the toes of appressed limbs. The tongue is not free anteriorly, but is capable of considerable extension.

Epaxial musculature (see Fig. 49).- The myomeres are of basic urodelan and plethodontid pattern, rising posteriorly from between adjacent vertebrae and with the deep posterior flexures inserting onto the dorsal surfaces of the posterior zygapophyses. *P. jordani* is, however, of more primitive aspect than many of the plethodontids described subsequently in that the anterior flexures are produced further forward. Well-developed hyperapophyseal muscles are present, each pair inserting on one of the posterodorsally extending, bifurcate, and plate-like hyperapophyses (see Fig. 14). The pattern and relationships of the myomeres of the *dorsalis trunci* are shown in Figure 49.

Hypaxial musculature (see Fig. 49).- The *subvertebralis* shows a markedly primitive construction, exhibiting features of hynobiids and ambystomatids, but also foreshadowing the more derived plethodontid condition. The septal pattern of each myomere is basically the same as in young metamorphosed *Rhyacotriton* (q.v.), but the pattern of the muscle fibers associated with the septa and of the attachment of septa to the vertebrae differs from other ambystomatids. Lateral to each intercentral joint a septum extends anteriorly and medially along the lateral edge of the anterior centrum. Based on positional relationships, this septum is homologous with the anterior basapophyseal septum of hynobiids and ambystomatids. However, it differs in attaching to the posterior basapophyseal area and in lacking internal muscle fibers joining it to the centrum. Rather, it retains only the external group of fibers, which extend anterolaterally to the next anterior myomere.

As in ambystomatids, a distinct posterior flexure extends back from each transverse process. However, the internal septum of each flexure extends anteromedially to the posterior cotyle of the next anterior vertebra. From each V-shaped flexure a long, relatively wide septum extends posteriorly. Fibers fan backwards from this into the next posterior flexure. Although homologous with the transverse process flexure of cryptobranchoids and ambystomatoids, this flexure is called the posterior flexure in plethodontids and salamandrids so as to emphasize the change in pattern that has occurred.

Comparison of this system with that of hynobiids shows the fundamental similarity and homology of structures. However, the area in which pull is concentrated on the centrum differs. In the more primitive ambystomatids and hynobiids with anterior basapophyses there is anterior and posterior pull on the anterolateral edges of the centra. In the more derived state, such as *P. jordani*, there is posterior and anterior pull on the posterolateral portions of the centra, at which point posterior basapophyses are liable to develop in larger individuals. Estes (1965b and pers. comm.) notes that larger individuals of *P. jordani* and *P. glutinosus* sometimes have both anterior and posterior basapophyses. If so, this could indicate that the association of the posterior flexure with the centrum is variable in placement. These species show all but perfect intermediate stages between the more primitive salamanders and the typical plethodontid condition, with *P. glutinosus* (see below) being somewhat more derived than *P. jordani* in terms of the *subvertebralis*.

In superficial ventral view the basic pattern of the *subvertebralis* is more or less obscured in *P. jordani*, owing to a layer of long muscle fibers covering the posterior flexures. Lateral to this region the myomeres descend anteroventrally from between adjacent ribs, such that each myomere partially underlaps its anterior neighbor. The most ventral muscle fibers, next to the peritoneum, extend anterolaterally in the main body of the myomere. This layer is thin and the fibers dorsal to it extend posterolaterally and, distally, blend into the *o. e. profundus*.

Adipose tissue is concentrated beneath each centrum, between the left and right halves of the *subvertebralis*. Each spinal nerve in the trunk proper exits intravertebrally, just behind the origin of a transverse process. From here they extend posterolaterally through the *subvertebralis*, paralleling the ribs. The nerves are exposed to the peritoneum near the lateral edge of the *subvertebralis* and then pass between the *transversus* and *o. e. profundus* along the posterior edge of each myoseptum in the lateral abdominal musculature.

Lateral abdominal musculature (see Fig. 49).- Except for one or two features, the musculature of this region is as in other plethodontids. Externally the *o. e. superficialis* covers the area between the *dorsalis trunci* and the *rectus abdominis*. The fibers of this unit extend dorsoventrally and are segmented by myocommata. A narrow *rectus lateralis* extends anteroposteriorly just below the epaxial myomeres and between the *o. e. superficialis* and *o. e. profundus*. The latter unit, deep to the *o. e. superficialis*, is a direct ventral continuation of the *subvertebralis*. Its fibers extend posteroventrally between adjacent myocommata, blending with the *rectus abdominis superficialis* ventrally. The *rectus abdominis* is divided into two parts: the simple *r. a. superficialis*, which is a very thin ventral band of fibers running anteroposteriorly between adjacent myocommata; and the *r. a. profundus* deep to it. Although blending with the *o. e. profundus*, the *r. a. superficialis* also sends a thin flap of muscle fibers over the former unit externally. In this it resembles certain of the more primitive ambystomatids.

The *r. a. profundus* is located between the *o. e. profundus* and the *transversus*, and dorsal to the *r. a. superficialis*. Unlike the other layers of lateral abdominal musculature, it is a discrete band set off from the other units. It extends between the hyobranchium and the pelvic girdle, as in many hynobiids and some salamandrids. This fact tends to indicate that the condition is primitive. The myosepta of the *r. a. profundus* produce a segmented band and the muscle fibers extending between are in two layers. The more external layer orients slightly anterolaterally, the fibers of the internal unit extend anteromedially.

The most internal layer of the body wall, the *transversus*, is composed of fibers proceeding anterolaterally and slightly underlaps the *r. a. superficialis* ventrally. Dorsally the *transversus* is invaded by myosepta for a short distance. This is presumably primitive and differs from the condition in most other plethodontids (compare hynobiids and ambystomatids). Some of the fibers of the *transversus* extend into the lateral edge of the *subvertebralis*, attaching to the anterior wall of each myoseptum in this area. As in the more primitive ambystomatids, the *o. internus* is lacking.

Plethodon glutinosus (Green 1818)

RANGE. Widespread in the eastern United States from "New York south to [the] northern half of Florida, the Gulf States to Texas, [and] northward . . . to northern Indiana" (Bishop 1943, p. 250).

HABITAT. "Usually found beneath logs and stones in woods, in crevices of shale banks, and along the sides of wooded gullies and ravines. Frequently occurs under moist humus [, being] . . . sensitive to dry air . . . and burrowing deeply in dry seasons" (Bishop 1943, pp. 250-251, see also Dunn 1926). Eggs are lain on land in moist, protected places and "guarded" by the female.

FOSSIL RECORD. This species is recorded from the Pleistocene of Florida (Holman 1958, 1959a,b).

RELATIONSHIPS. Assigned by Highton (1962, 1972) to the eastern large plethodon group, along with *P. jordani* (q.v.) and other species not described. Discussion of specific relationships within the genus are given above.

REMARKS. The form of the body and tail of *P. glutinosus* is almost identical to that of *P. jordani*. However, on average, the trunk seems somewhat longer, there being almost invariably 16 costal grooves (vs. 15 as the average in *P. jordani*).

Epaxial musculature (see Fig. 50).- The *dorsalis trunci* is as in *P. jordani*, but with the anterior flexures somewhat shorter and broader, and the septum supporting the hyperapophyseal muscle much broader and less elongate. As in *P. jordani*, elongated deep posterior flexures insert onto the dorsal surfaces of the postzygapophyses.

Hypaxial musculature (see Fig. 50).- The *subvertebralis* differs somewhat from that of *P. jordani*, but the same plan is evident. The differences of *P. glutinosus* are relatively minor and the condition is readily derivable from that of *P. jordani*.

The posterior flexures have come to be appressed against the lateral edges of the centra. The flexures have the apices at the level of the posterior cotyle of the associated vertebra. From each apex a long, relatively broad septum extends back to just behind the proximal edge of the transverse process of the next posterior vertebra. Muscle fibers fan from this septum: some extend posteromedially to the lateral border of the centrum, others run posteromedially and posterolaterally into the succeeding posterior flexure. The internal septa seen in *P. jordani* (presumably homologous to the anterior basapophyseal septa) are lost in *P. glutinosus*, which has muscle fibers extending directly onto the centra.

P. glutinosus is an ideal intermediate between *P. jordani* and the more derived plethodontids such as *Eurycea* and *Gyrinophilus*. A morphocline (see Fig. 90) uniting ambystomatids and derived plethodontids shows clearly how the restructuring of the *subvertebralis* took place. The change is seen to have been gradual, each stage remaining functional, with many of the stages having been maintained into the present. If these intermediates had become extinct, the condition in desmognathines (q.v.) would seem radically different from that of ambystomatids. Although how the change occurred is evident, the reasons why are not certain. Detailed functional morphological study is necessary to elucidate the matter.

Lateral abdominal musculature (see Fig. 50).- This unit has not been found to differ from the condition in *P. jordani*.

Plethodon cinereus (Green 1818)

RANGE. Found in the northeastern United States and southern Canada, with disjunct populations in Missouri, Arkansas, Oklahoma, Georgia, North Carolina, Minnesota, and about the southern tip of James Bay in Ontario (see Smith 1963).

HABITAT. Found "within rotten logs and stumps, under objects on the ground, and in forest-floor litter in relatively cool and mesic coniferous and hardwood forests" (Smith 1963, p. 5.1). There is no larval stage and the female broods the eggs.

FOSSIL RECORD. None known.

RELATIONSHIPS. A member of the eastern small plethodons (*P. cinereus* group) of Highton (1962, 1972), which also include the species *hoffmani*, *richmondi*, *shenandoah*, *hubrichti*, *nettingi*, *dorsalis*, and *welleri*.

Although generally considered along with the western plethodons to be the most primitive within *Plethodon*, this cannot be upheld. At least as regards the structure of the vertebrae and the trunk musculature, the eastern large plethodons are more primitive.

REMARKS. These are small elongate salamanders with diminutive limbs. The trunk and tail are rounded and slender. There is great variability in the numbers of trunk vertebrae, depending on the geographic locality of the subspecies concerned. Recorded counts (from Highton 1962) are as follows:

P. cinereus cinereus: modal number 19, 20, or 21, depending on locality.

P. c. serratus: modal number 20.

P. c. polycentratus: modal number 21 or 22.

The trunk vertebrae range in number from 17 to 24, with 20 being the most common count (Highton 1962, p. 291). This is unusually high variability for salamanders.

Counts for some of the other eastern small plethodons are given below, with the most common number underlined:

P. welleri: 16-17-18

P. dorsalis: 18-19-20

P. richmondi: 18-19-20-21-22-23-24

It would be productive to carry out natural historical and functional morphological studies on these salamanders to determine the adaptive significance of the variation.

Differences of *P. cinereus* from the other species of *Plethodon* here described are slight and only the *subvertebralis* is discussed.

In the development of the trunk musculature, cranial osteology, overall form, and biogeography, *P. cinereus* is an acceptable structural ancestor for *Hemidactylium* and also *Eurycea*.

Hypaxial musculature.- The *subvertebralis* of this species is developed as in the larger *P. glutinosus*. It is, therefore, more derived than in the representative of the western plethodons (*P. vehiculum*) described below. The posterior flexure is closely associated with the postero-lateral edge of the centrum. From the apex of each flexure (just lateral to the posterior cotyle of the associated centrum) a septum extends posteriorly. Muscle fibers fan from this septum, forming the body of the following posterior flexure. The *transversus* extends into the lateral edge of the *subvertebralis* in a manner very similar to the condition in *Eurycea*.

Plethodon vehiculum (Cooper 1860)

RANGE. Known from "western Oregon, Washington, and [southwestern] British Columbia including Vancouver Island" (Bishop 1943, p. 278).

HABITAT. Found on "rocky outcrops and talus of fine-grained sandstone and shales" in the Coast Range of the Rockies, and "during the moist season it can be found under the bark of and in decaying logs, under ground cover, and within cleavage planes among dead leaves" (Storm and Brodie 1970, pp. 83.1-83.2). Eggs are lain on land and attended by the female.

FOSSIL RECORD. None known.

RELATIONSHIPS. According to Highton (1962) this species is closest to *P. dunni*, with these two species grouped along with *P. vandykei*, *P. larselli*, and *P. elongatus* in the western plethodons. This group was believed to be most closely related to the eastern small plethodons (e.g., *P. cinereus* and *P. dorsalis*), and both groups were held to be more primitive than the eastern large plethodons. Features used in Highton's (1962) analysis included coloration, tooth counts, number of trunk vertebrae, and degree of body elongation. These features are extremely variable within the Caudata and cannot be accorded significant weight. Indeed, I would argue that they are generally useless in the determination of relationship and phylogenetic status.

In vertebral structure (long and low vertebrae) and higher numbers of trunk vertebrae, features used by Highton (1962), the eastern small and the western plethodons are derived with respect to the eastern large plethodons. In terms of the *subvertebralis*, *P. vehiculum* is more primitive than *P. cinereus*, however. Whereas Highton's groupings have validity, at least as descriptive units, his interpretation of morphoclinal polarity is all but certainly incorrect. The western plethodons are probably derived from stock represented by the eastern large plethodons, independently of the eastern small plethodons.

Brodie (1970) has divided the western plethodons into three species groups: the primitive *vandykei* group (*P. vandykei* and *P. larselli*), the intermediate *vehiculum* group (*P. vehiculum*, *P. dunni*, and *P. gordoni*), and the most "advanced" *elongatus* group (*P. elongatus* and *P. stormi*). On the basis of having the longest legs, the widest head, the fewest vertebrae, and the highest number of vomerine and premaxillary teeth, *P. vandykei* was considered the most primitive of the western plethodons.

REMARKS. *P. vehiculum* is an elongate *Plethodon*, but with a relatively robust trunk (compare *P. neomexicanus* and *P. cinereus*) and a thin, relatively short tail. The usual number of trunk vertebrae is 17, but counts of 16 and 18 also occur (Highton 1962). Western plethodons show considerable variation in numbers of trunk vertebrae (i.e., *P. vandykei*: 15-16; *P. larselli*: 15-17; *P. dunni*: 16-17; *P. elongatus* 18-20), but much less than is encountered in the eastern small plethodons. Limbs in *P. vehiculum* are small, but relatively robust.

Epaxial musculature (see Fig. 51).- The *dorsalis trunci* is developed as in *P. jordani*, but differs in the lesser development of deep posterior flexures. This may be an allometric phenomenon associated with differing body size.

Hypaxial musculature (see Fig. 51).- The *subvertebralis* is very like that of *P. jordani*. Posterior flexures have muscle fibers extending posteromedially onto the lateral surface of the adjacent centra. In this feature *P. vehiculum* and *P. jordani* are more similar than either is to *P. glutinosus*. Unlike the situation in either *P. jordani* or *P. glutinosus*, however, this species has the spinal nerves buried completely within the *subvertebralis*. In overall structure of the hypaxial musculature, *P. vehiculum* is more primitive than the other species of *Plethodon* described here, excepting *P. jordani*. This does not indicate special relationship between the two species, as resemblances are subtle and, presumably, owing to the retention of primitive features.

Lateral abdominal musculature.- The lateral abdominal musculature is associated with the *subvertebralis* as described in *P. jordani* and *P. glutinosus*. There is no discernable difference between *P. vehiculum* and *P. jordani* as regards the structure of this unit.

Plethodon neomexicanus Stebbins and Riemer 1950

RANGE. Known only at "elevations of from 7200 to 9200 feet . . . in the Jemez Mountains of . . . New Mexico" (Williams 1973, p. 131.1).

HABITAT. Found in "mixed coniferous forests . . . primarily on north-facing slopes under rocks and in and under rotting logs" (Williams 1973, p. 131.1). There are frequent summer rains in the range, during which the animals are active on the surface, and heavy winter snows. There is an understory of herbs and scattered clumps of grass; streams and ponds are rare. The rotting logs inhabited by *P. neomexicanus* are shared with an abundant invertebrate fauna (Stebbins and Riemer 1950), but specimens available to me had only ants in the gut.

FOSSIL RECORD. None known.

RELATIONSHIPS. Highton (1962) associated this species with the eastern small plethodons (e.g., *P. cinereus*). Muizuno and MacGregor (1974), however, determined on the basis of DNA sequences held in common that, whereas other members of the genus clustered into Highton's groupings, *P. neomexicanus* was distinctive. These authors proposed that the Jemez Mountain salamander was an early derivative from eastern small plethodon stock prior to the split of the western and eastern large plethodons. Although distinct from the western plethodons, *P. neomexicanus* is probably closer to the eastern large plethodons than to the eastern small plethodons. This would be the conclusion based on comparative anatomy and, as the significance of DNA studies is problematical, this relationship may be accepted as most reasonable at present. I place *P. neomexicanus* in its own monotypic species group derived from the eastern large plethodons (*P. glutinosus* group).

REMARKS. These salamanders are relatively large in comparison to members of the eastern small plethodon group. The trunk is elongate, but quite robust, whereas the tail is long and heavy. The usual number of trunk vertebrae is 20, with counts of 19 and 21 encountered more rarely (Highton 1962). These correlate with costal groove counts of 18, 19, and 20. The eyes are large and protuberant. Limbs are small, but not diminutive.

Epaxial musculature (see Fig. 52).- The *dorsalis trunci* is similar to that of the other species of *Plethodon*. Anterior flexures are elongate and provided with anteriorly directed septa. Hyperapophyseal muscles are small and narrow. Unlike members of the *P. glutinosus* group, deep posterior flexures are seemingly lacking throughout the column. Deep posterior extensions from the lateral surface of the main bodies of the myomeres are present and especially well developed immediately presacrally, but these do not come to insert on the vertebral column directly, although muscle fibers do provide an attachment. As in the *P. glutinosus* group, but different from *P. vehiculum*, the epaxial myomeres extend distal to the ribs.

Hypaxial musculature (see Fig. 52).- The *subvertebralis* differs from that of *P. jordani*, being similar to that of *P. glutinosus*. Posterior flexures are closely associated with the posterior edges of the centra, producing direct pull on the posterior basapophyseal regions. Small posterior basapophyses are present, providing areas of insertion for the medial septa of the posterior flexures. Muscle fibers fan posteromedially and posterolaterally from these septa, forming the bodies of the posterior flexures. The main body of each myomere is thin, barely covering the ribs ventrally. A single layer of muscle fibers extends anterolaterally, just beneath the ribs. Intercostal fibers run posterolaterally and are continuous with the *o. e. profundus* distally and ventrally.

Spinal nerve exits are as in *P. jordani*, with the nerves extending ventrolaterally to the peritoneal surface of the *subvertebralis*. They are exposed to the peritoneal cavity for a short distance, but are located between the *transversus* and the *o. e. profundus* more distally.

Lateral abdominal musculature (see Fig. 52).- Although the lateral abdominal musculature is composed of the same units as in the species of *Plethodon* described above, the relationships differ somewhat. The *o. e. superficialis* is a narrow band running between the limb girdles; the band is segmented by myosepta and composed of muscle fibers extending dorsoventrally between these septa. In *P. neomexicanus* the *o. e. superficialis* barely overlaps the *rectus lateralis*, falling short of the epaxial myomeres, thereby differing from *P. jordani*, and being most similar to *P. vehiculum*. Ventrally the *o. e. superficialis* extends just over onto the *rectus abdominis*.

As in other species of the genus, a *rectus lateralis* is present. The *o. e. profundus* is a direct continuation of the intercostal muscles and blends with the *r. a. superficialis* ventrally. The *o. internus* is absent and the two units of the *rectus abdominis* are developed as in *P. jordani*. The relationship of the *transversus* to the *subvertebralis* differs considerably in *P. neomexicanus*, however. Whereas in the other species the *transversus* extends partially into the *subvertebralis*, in the Jemez Mountains salamander it is applied against the ventral surface of the *subvertebralis* in a manner similar to the condition in certain ambystomatids. This is, presumably, paedomorphic as it resembles the situation of larval salamanders generally, but differs from that of other adult plethodontids. In correlation with this difference, the ventral layer of the *subvertebralis* extends a short distance into the lateral abdominal musculature, foreshadowing the development of a true *o. internus*.

Ensatina eschscholtzii Gray 1850

RANGE. Found in the "mountains of the Pacific Coast from the southwestern mainland and Vancouver Island, British Columbia, south to extreme southern . . . California" (Stebbins 1962, p. 87).

HABITAT. Common in areas where leaf litter is abundant, "under boards, logs, rocks, in refuse heaps, leaf litter, under bark, and inside logs . . . . Understory vegetation is often scarce" in the frequented forested areas and "a perennial stream is often present although it is not a necessity" (Stebbins 1962, pp. 94-95). Individuals are capable of burrowing only through leaf litter and very loose soil, and spend considerable time on the surface during damp, cool weather. *Ensatina* is strictly terrestrial, with eggs being laid on land.

FOSSIL RECORD. None known.

RELATIONSHIPS. Dunn (1926) considered the monotypic *Ensatina* to be close to *Plethodon*, differing only in minor features. Wake (1966) suggested that it was derived from the *P. vehiculum* group, a conclusion not controverted by my studies. Until Stebbins' (1949) excellent study several species of *Ensatina* were recognized, but he showed that these were simply local races differing in distinctive colour patterns, but otherwise similar and intergrading.

REMARKS. Both young individuals (s. v. length just over three cm) and larger adults were dissected. The small specimens have short, slender bodies. The limbs are long and powerful, overlapping when appressed. The tail is relatively short and oval in cross-section, with breakage occurring at the basal constriction. One of the small individuals was gravid. In fully grown individuals the trunk is proportionally longer and relatively robust. The limbs are still large and powerful, and the tail is robust and long. The trunk musculature shows little ontogenetic variation, except for the *dorsalis trunci*.

The gait of this salamander is unusual. "The animal seems to walk crocodilelike with the body held relatively high, the tail scarcely touching the ground or not at all. This is done slowly, methodically, and with no lateral undulation of the body" (Peabody 1959, p. 11).

Epaxial musculature (see Figs. 53 and 54).- The *dorsalis trunci* resembles that of *Plethodon*. In small specimens in dorsal view parts of the cartilage caps on the hyperapophyses are visible along the column. In larger individuals the hyperapophyses are finished in bone and buried in musculature. Anterior flexures are relatively blunt, becoming longer in adults and being provided with well-developed septa extending anteriorly and paralleling the hyperapophyseal muscles below. Hyperapophyseal muscles seemingly lack septa in the small specimens, but with the formation of the bony hyperapophyses in adults vertical septa extend posteriorly from each hyperapophysis to serve as areas of attachment for musculature.

Small individuals have well-developed deep posterior flexures extending posteromedially from the main bodies of the myomeres to insert on the anterior edges of the postzygapophyses of the following vertebrae. These flexures are, however, lacking from the larger specimens available to me. Without larger sample sizes and more detailed study, the significance of this remains obscure.

A relatively small mass of musculature is in the main body of each myomere. The myomeres rise very acutely posteriorly from between adjacent ribs. In the small individuals superficial fibers of these areas extend anterolaterally, whereas the deeper fibers run anteroposteriorly. In larger individuals all fibers tend to extend anteroposteriorly.

Hypaxial musculature (see Figs. 53 and 54).- The *subvertebralis*, although differing somewhat from that of *Plethodon*, is extremely similar and readily derivable from that genus. Posterior flexures extend from each transverse process, with a very long, wide septum running back from the apex of each. This septum is relatively broader in the larger specimens. The posterior flexures terminate anterior to the posterior cotyle of the associated vertebra. The posterior septa give rise to fan-shaped muscles, which extend into the following posterior flexures. The muscles of this system are thin and not associated with the posterior basapophyseal region of the centra. As expected from the conformation of the musculature, posterior basapophyses are lacking.

The main bodies of the subvertebral myomeres have the most ventral fibers extending posterolaterally, whereas the more dorsal ones run posterolaterally. The myomeres descend anteroventrally from between adjacent ribs, each myomere slightly underlapping its anterior neighbour distally.

Spinal nerves exit intravertebrally, running posterolaterally through the *subvertebralis* and then between the *transversus* and *o. e. profundus*. Smaller specimens do not have the nerves exposed to the peritoneum, but in larger ones a slight exposure is seen at the lateral edge of the *subvertebralis*.

Lateral abdominal musculature (see Figs. 53 and 54).- The muscles of this region are the same in both large and small *Ensatina*, being developed according to the basic plethodontid plan. As in *Plethodon*, the *o. e. superficialis* is composed of muscle fibers extending dorsoventrally parallel to the segmenting myocommata. In larger specimens it does not quite reach the *dorsalis trunci* above. Deep to this the fibers of the *o. e. profundus* extend posteroventrally between the myocommata. This unit is a direct ventral continuation of the subvertebral musculature and blends with the *r. a. superficialis* below. There is no *o. internus*.

As are the other layers, the internal *transversus* is relatively thin. It is quite wide, underlapping much of the *r. a. superficialis*.

The muscle fibers extend anteroventrally, extending part way into the *subvertebralis* dorsally, with certain fibers curving posteriorly to insert on each rib. The dorsal part of the *transversus* is invaded by short myoseptal extensions, the remainder being undivided.

The *r. a. superficialis* has fibers extending anteroposteriorly. There is no external flap applied against the *o. e. profundus* as was seen in *Plethodon*. Dorsal to the *r. a. superficialis*, and between the *transversus* and *o. e. profundus*, is found the free *r. a. profundus*, which extends between hyobranchium and pelvis. It is not readily divisible into deep and superficial layers as in other plethodontids. In the smaller individuals the *r. a. profundus* is very wide anteriorly, but this is not the case in the larger specimens.

Aneides lugubris (Hallowell 1849)

RANGE. Found in western California along almost the entire coastal region and a significant distance inland. Populations are also known from various offshore islands (Bishop 1943).

HABITAT. This species is largely arboreal, but often is found on the ground "in logs and stumps or beneath surface materials . . . eggs have been discovered both in the soil and in the cavities of trees" (Bishop 1943, pp. 340-341).

FOSSIL RECORD. None known for the species or genus.

RELATIONSHIPS. *Aneides* is derivable from *Plethodon*, as shown by Dunn (1926) and Wake (1966). Dunn (1926), Lowe (1950), and Gordon (1952) all considered *Aneides aeneus* to be the most primitive living member of the genus. Wake (1963), however, argued that *A. hardii* was the most primitive, although closely related to *A. aeneus*. At the same time, he divided the genus into the following species groups:

A. hardii group: monotypic.

A. aeneus group: monotypic.

A. lugubris group: *A. lugubris*, *A. ferreus*, and *A. flavipunctatus*.

Wake (1963) believed that the *A. lugubris* group is the most derived, a conclusion confirmed by my studies, and that it was an early derivative of the *A. hardii* group, prior to the split of *A. aeneus*.

REMARKS. *A. lugubris* is a large, powerfully built salamander with robust limbs. The trunk is relatively short (usually 14 costal grooves, with counts of 13 and 15 also found), slender, and somewhat compressed dorsoventrally. The tail is long and slender. In males the mandibular musculature is greatly enlarged, giving a bulbous appearance to the posterior part of the head. In comparison to *Plethodon*, the trunk musculature is of relatively small mass. A tough layer of connective tissue binds the skin to the muscle fibers beneath. The vertebrae (see Fig. 14) are similar to those of *Plethodon*, but with development of a subcentral keel, large ventral lamellae, and a high neural crest.

Epaxial musculature (see Fig. 55).- The mass of the *dorsalis trunci* is reduced, but the pattern of the myomeres is basically as in *Plethodon* and *Ensatina*. Anterior flexures are long, extending almost half-way over the roofs of the anterior vertebrae of the pair spanned by their respective myomeres. Muscle fibers fan forward from the apex of each flexure, at which point an accessory septum extends anteriorly. The main body of each myomere rises steeply posterodorsally from between adjacent ribs. The superficial fibers of this part of the epaxial complex run anteriorly and slightly laterally between the myosepta. Deeper fibers extend anteroposteriorly.

As in *Plethodon*, deep posterior flexures are present. Each hyperapophysis gives rise to a pair of posteriorly directed septa. Muscle fibers extend from these septa onto the roof of the following vertebra. These hyperapophyseal muscles are associated with the anterior flexures dorsal to them. In larger individuals the hyperapophysis is bifurcate and finished in bone, providing stronger attachment for the associated musculature. Younger individuals have a cartilage cap in this area and the hyperapophyseal septa are much shallower and narrower.

Hypaxial musculature (see Fig. 55).- Whereas the *dorsalis trunci* resembles that of *Plethodon* and *Ensatina*, the *subvertebralis* is notably derived. In some respects it is similar to that of certain salamandrids, doubtless owing to convergence or (see Conclusions) parallelism. A well-developed ventral lamella is present on each transverse process (see Fig. 14), correlated with the modifications in the *subvertebralis*. Larger specimens show a weak opisthocoely.

The mass of the *subvertebralis* is markedly reduced in comparison to *Plethodon* and the undersides of the centra are not covered by musculature. Muscle fibers arise from the posterior edge of each ventral lamella and attach to the lateral edge of the centrum of the following vertebra. Upon removal of this layer the posterior basapophyseal septum is evident. This inserts on the posterolateral edge of the centrum, at which point the ventral lamella joins the centrum. From here the broad septum extends posteriorly and slightly laterally beneath the next posterior ventral lamella. Muscle fibers extend onto the ventral surface of the lamella from the septum.

The main bodies of the myomeres, ventral to the ribs, are very thin. The superficial fibers extend anterolaterally, with those of one myomere running under the anterior rib and partially under the next anterior myomere. The proximal parts of the ventral rib-heads and the distal parts of the transverse processes are not covered by muscle fibers. The *subvertebralis* does not extend laterally beyond the tips of the ribs. Above the ventralmost fibers the muscle strands align posterolaterally between adjacent ribs. These intercostal fibers blend indistinguishably with the *o. e. profundus* laterally.

Spinal nerves in the trunk region, excepting those of T1 and one pair associated with T2, exit from the spinal cord through the wall of the neural arch just posterior to the latter's union with the transverse processes. From here the nerves arch posterolaterally, coming to run along the ventral surface of the *subvertebralis* distal to the tips of the transverse processes. The nerves then meet the posterodistal tips of the ribs and then extend between the *transversus* and *o. e. profundus*. The marked exposure of the nerves to the peritoneum differs from most other plethodontids, although there is slight exposure in *Plethodon* and long exposure in *Hemidactylium*.

Lateral abdominal musculature (see Fig. 55).- The lateral abdominal musculature is typically plethodontid and the *o. internus* is absent. Beneath the skin, the surface of the trunk is covered by a thick layer of connective tissue. Internally, in contrast to species described previously, there is an extremely dense peritoneal lining.

Laterally the most external layer is the well-developed *o. e. superficialis*, which partially overlaps the *dorsalis trunci* above and the *rectus abdominis* below. Its muscle fibers are very slightly offset from the vertical. The *o. e. profundus* is as in *Plethodon*. The most internal layer, the *transversus*, is not segmented by myocommata. Several fibers arise from the anterior edge of each rib tip and the remainder originate along a line of connective tissue joining the tips of adjacent ribs. The *transversus* is thick, with the fibers extending anteroventrally to a point just beyond the dorsal edge of the *r. a. superficialis*. The *rectus abdominis* is divided into two parts, as in other plethodontids and the *r. a. superficialis* overlaps the *o. e. profundus* externally as described for *Plethodon jordani*.

Aneides aeneus (Cope and Packard 1881)

RANGE. Found in scattered areas in "the Allegheny and Cumberland Mountains from Pennsylvania to Alabama and northeastern Mississippi . . . [and] in the southern Blue Ridge Mountains of North Carolina, South Carolina, and Georgia," as well as in isolated pockets in Ohio (Gordon 1967, p. 30.1).

HABITAT. Restricted to relatively high elevations in the Appalachians in "damp but not wet crevices in shaded rock outcrops and ledges, as well as beneath bark and cracks of trees in cove hardwood forests" (Gordon 1967, p. 30.1). Dunn (1926) notes that *A. aeneus* is sometimes found in association with *Plethodon glutinosus*. Eggs are laid terrestrially and are brooded.

FOSSIL RECORD. None known.

RELATIONSHIPS. Dunn (1926) and subsequent workers considered this species to be the most primitive *Aneides*. Lowe (1950) thought there had been a split into the eastern species (*A. aeneus*) and western species during Miocene time on the basis of botanical evidence. Wake (1963), however, believed *A. aeneus* to be derived with respect to *A. hardii*, although the two were considered to be closely related. *A. aeneus* is relatively primitive in almost all features in comparison to the other species of *Aneides*; but *A. hardii* has not been available for comparisons of the trunk musculature to be made.

REMARKS. All available specimens had 14 costal grooves, counting one in the axilla and one in the groin. Gordon (1967) notes counts of 15 for some specimens. Although Gordon stated that the jaw musculature (especially of males) is "greatly" enlarged, neither Dunn (1926) nor Bishop (1943) mention this characteristic. Specimens available to me do not have a swollen temporal region. The elongate, flattened premaxillary teeth seen in other *Aneides* are absent.

The trunk is thin, but not elongate and the tail is long, thin, and rounded in cross-section. The head and body are flattened dorsoventrally. Terminal phalanges are T-shaped, as in other *Aneides*, and the limbs are long and relatively thin. Only the hypaxial musculature is described, as the other units are like that of the other species of *Aneides* that were dissected.

Hypaxial musculature.- The ventralmost layer of the *subvertebralis* is composed of muscle fibers extending anteroposteriorly. Dorsal to this single layer the intercostal fibers extend posterolaterally. In contrast to *A. lugubris*, posterior flexures are definitely present, although weakly developed. Immediately behind the pectoral girdle, where they are most strongly developed, the posterior flexures do not quite reach to the edge of the associated posterior cotyle. A septum extends posteriorly from the rear end of each flexure. Muscle fibers fan backwards from these septa, forming the bodies of the following posterior flexures. In the posterior region of the trunk the flexures undergo marked reduction. The two or three immediately presacral myomeres extend intercostally between only two vertebrae, with no overlap or posterior flexure present. The *transversus* is a thin sheet extending anteroventrally at an angle only slightly displaced from the vertical. It is not divided at any point by myocommata, and the basic situation is as in *A. lugubris*.

Aneides ferreus Cope 1869

RANGE. Found on Vancouver Island, British Columbia and southward in coastal Oregon and northernmost California (Dunn 1926, Wake 1965).

HABITAT. In contrast to *A. aeneus*, this species is found at low elevations and in relatively diverse habitats. "It inhabits redwood, Douglas fir, and other coniferous forests . . . [and] is found most frequently under the loose bark of fallen logs in small clearings or at the margins of forests." It is partially arboreal and also "locally abundant in small rock slides and in moist rock crevices" (Wake 1965, p. 16.1).

FOSSIL RECORD. None known.

RELATIONSHIPS. Dunn (1926) allied *A. ferreus* with *A. lugubris*. Wake (1965) grouped it with *A. flavipunctatus* and *A. lugubris* in the *A. lugubris* group, which was considered the most derived of the genus.

REMARKS. The trunk is somewhat more robust than that of *A. aeneus* and the body less flattened. The trunk has a greater number of vertebrae, costal groove counts being 16 or 17. The tail is also proportionally shorter. Toe pads are present, as in other *Aneides*. The premaxillary teeth of males are not notably enlarged, but they may perforate the lips in some individuals (see Bishop 1943).

The trunk musculature differs in no significant way from that of *A. aeneus*, except that the posterior flexures of the *subvertebralis* are somewhat larger. For this reason a description is not provided.

Hemidactylium scutatum (Schlegel 1838)

RANGE. Widespread in the eastern United States and southern Ontario, with isolated occurrences in Missouri, Arkansas, Louisiana, Georgia, Florida, and throughout Nova Scotia. The distribution within these regions is disjunct, being limited to areas that provide suitable adult and larval habitat in close proximity (Neil 1963).

HABITAT. Adults are terrestrial "under stones, logs, wood slabs, leaf litter, or moss in beech and maple, yellow birch and maple, and other hardwood forests, [and] less often in coniferous forests. . . . The larval life is spent in pools, bogs, or slow bog streams with an abundance of sphagnum, other mosses, hepatics, and sedges" (Neil 1963, p. 2.1). Eggs are laid in sphagnum moss close to standing water and are brooded by the female. Upon hatching, the larvae enter the water for a short period. The aquatic larval phase is almost certainly secondary (see Dunn 1926).

FOSSIL RECORD. None known.

RELATIONSHIPS. Dunn (1926, pp. 201-203) considered *Hemidactylium* to be closely related to *Plethodon* and to possess aquatic larvae secondarily: "The situation is . . . obviously secondary . . . and the resemblance [to *Ambystoma* and *Triturus*] is convergence and looks very much like a case of reversed evolution, the larva of the specialized *Hemidactylium* taking on the characters of the larva of forms more primitive than any of its own immediate ancestors." Piatt's (1935) studies on the hyobranchial apparatus of plethodontids confirmed Dunn's conclusions, although Tanner (1952) disagreed.

Wake (1966) placed *H. scutatum* with the *Eurycea* group of plethodontids, but provided no evidence controverting Dunn's (1926) hypothesis of the secondary nature of the aquatic larva of *Hemidactylium*. Dunn's concept is evidenced by osteology, trunk musculature, the fixed tongue, and the "apparently primitive but really highly specialized . . . nature of . . . [the] aquatic larval stage" (Dunn 1926, p. 203). Wake and Lombard (1973), on the basis of the hyobranchial apparatus, suggested that *Hemidactylium* was an early, independent offshoot of plethodontid stock. This is close to my conclusion, with *Plethodon* being representative of this basal stock.

REMARKS. This is a small salamander with a thin, long trunk. There are 13 or 14 costal grooves, not a high number for a plethodontid, especially in view of the length of the trunk. The tail is very long and heavy, and provided with an area of weakness just posterior to the cloaca. The limbs are very small, but actively and efficiently used in normal locomotion. At such times the trunk is held straight and the animal walks without lateral undulations. During stress, locomotion over land becomes snake-like, with the limbs held against the body and clear of the substrate. The adult avoids water, becoming very agitated if forced into an aquatic situation.

Epaxial musculature (see Fig. 56).- The skin is thick and strongly bound to the trunk musculature. Epaxial myomeres and, especially, the lateral abdominal musculature are difficult to preserve during removal of the skin. The *dorsalis trunci* needs little description, being very similar to that of *Plethodon*. Anterior flexures are short and blunt, and lack anteriorly projecting septa from the apices. The main body of each myomere rises steeply posteriorly from between adjacent ribs. There are deep posterior flexures present, but these are small and poorly supplied with musculature. Hyperapophyseal muscles are present, but ill-defined and hyperapophyseal septa are seemingly absent. The *dorsalis trunci* extends a short distance beyond the distal tips of the ribs. Muscle fibers in the main bodies of the myomeres are almost exclusively aligned anteroposteriorly.

Hypaxial musculature (see Fig. 56).- The *subvertebralis* differs somewhat from that of *P. glutinosus* and *P. cinereus*, but is readily derivable from such structural ancestors. In ventral view the presence of posterior flexures is not evident, owing to the presence of an obscuring layer of fibers underlying them. When the thin medial layer of anteroposterior fibers is removed, small but well-developed posterior flexures from the transverse processes are evident. These are composed of a septum extending posteromedially from the distal part of each ventral rib-bearer to the lateral edge of the posterior cotyle of the same vertebra. Each flexure sends a small septum back into the following flexure. This septum is also associated with the posterior basapophyseal region of the centrum and, with its muscle fibers, could be said to constitute an incipient posterior basapophyseal muscle. These muscles are not developed to the same extent as those in the *Eurycea* and *Desmognathus* groups.

Lateral to the posterior flexures, the *subvertebralis* is thin, covering the ribs with only a thin layer of muscle fibers ventrally. The fibers of the ventral layer extend anterolaterally and overlap the *transversus* at the distal edge of the *subvertebralis*. The main body of each myomere is inclined slightly anteriorly in undistorted specimens. Intercostal muscle fibers extend posterolaterally, blending into the *o. e. profundus*.

The spinal nerves exit intravertebrally and extend posterolaterally through the *subvertebralis*. They are exposed for some distance on the peritoneal surface and then extend between the *transversus* and *o. e. profundus* as in other plethodontids.

Lateral abdominal musculature (see Fig. 56).- The muscle layers forming the lateral and ventral walls of the visceral cavity are extremely thin, with only the *r. a. profundus* and lateral parts of the *r. a. superficialis* being formed of more than a single layer of fibers. The *o. e. superficialis* is relatively wide, overlapping the *dorsalis trunci* above and, by means of fascia, the *rectus abdominis* ventrally. Its fibers extend dorsoventrally, paralleling the segmenting myocommata, but with a very slight posteroventral component, especially in the posterior portion of each myomere.

The *o. e. profundus* is as in *Plethodon*, although blending almost imperceptibly with the *r. a. superficialis* ventrally. The *o. internus* is absent and the *transversus* is not quite so thin as the two layers of the *obliquus externus*. The *transversus* is as in *Plethodon*, with the dorsal fibers bending posteriorly to attach to the distal tips of the ribs. Ventrally there are areas of tight attachment to the myosepta of the *rectus abdominis*. Dorsally the *transversus* is invaded for a very short distance by myosepta. The two layers of the *rectus abdominis* are developed as in *Plethodon*, but the *rectus lateralis* is absent.

Batrachoseps attenuatus (Eschscholtz 1833)

RANGE. Found along the west coast of North America from southernmost Oregon, through California, and into northern Baja California (Stebbins 1962).

HABITAT. "The Upper Sonoran and Transition life-zones, in moist situations on the ground, in leaf litter and beneath surface objects . . . . In dry weather, [the species] retreats underground" (Stebbins 1962, p. 109). Eggs are laid on land and apparently are not brooded (Maiorana 1976), but other species of *Batrachoseps* brood (see Salthe and Mecham 1974).

FOSSIL RECORD. Peabody (1959) described upper Pliocene trackways from

California that he demonstrated as most probably made by a species of *Batrachoseps*. Brame and Murray (1968) believed these trackways to be referable to the living *Batrachoseps relictus*, but this is problematical.

RELATIONSHIPS. Dunn (1926) and Tanner (1952) considered *Batrachoseps* to be closely allied to the *Plethodon* group, with which it shares a fixed tongue. Piatt (1935), Wake (1966), and Brame and Murray (1968) believed it to be related to *Bolitoglossa* and its allies. In view of the fixed tongue in *Batrachoseps*, the only possibility of bolitoglossine relationship is by derivation from an early stock prior to the origin of the free tongue in the bolitoglossines proper. Wake's (1966) suggestion of derivation from the supergenus *Bolitoglossa* after the latter split from *Hydromantes* is illogical, as it demands secondary loss of the free tongue in *Batrachoseps*. As regards vertebral structure, *Batrachoseps* is similar to *Plethodon*, whereas the *subvertebralis* converges upon some of the bolitoglossines. I believe *Batrachoseps* to be most nearly allied with the western plethodons, as argued by Dunn (1926) and Tanner (1952).

Brame and Murray (1968) have conducted the most recent revision of the genus, recognizing seven species, with *B. wrighti* and *B. relictus* being the most primitive. The following features were held to be primitive: short trunk with 16-17 costal grooves, moderately long limbs, nonfossorial habits, separate premaxillae, presence of prefrontals, high percentage of nucleated erythrocytes, vomerine teeth in single rows, and large males with multiple testes. *B. wrighti* was seen as an early derivative from *B. relictus*, while the remaining five species arose from the latter at a later date. The time of origin of the genus was suggested as late Eocene, but data bearing on the question are almost nonexistent.

B. attenuatus and *B. major* are "the two most recently derived and most highly adapted [sic] species" (Brame and Murray 1968, p. 30). They have invaded a new zone of fossorial to subfossorial habit, have longer bodies and tails, and possess reduced heads and limbs. Brame and Murray argued that these two species left the ancestral Arcto-Tertiary geofloral association for the semi-arid Madro-Tertiary community. Unfortunately, only *B. attenuatus* has been available for study so that whether or not the structure of the trunk musculature is the same throughout the genus is not known.

REMARKS. *B. attenuatus* is a small, terrestrial salamander with a thin, elongate body and a very long, relatively robust tail. There is tail autotomy, but not localized as in certain other plethodontids. The limbs are diminutive. Peabody (1959) studied the locomotion of this species, noting (p. 11) that "on most sedimentary surfaces suitable for impression the inadequate [sic] limbs operate laboriously," and that it shows "little sinuous movement . . . the extreme of rigidity . . . [being] exhibited by tiny *Batrachoseps*, which walks somewhat like two men carrying a long pole" (p. 18). When locomotion is difficult or hurried, however, sinuous movement is pronounced. There are usually 20 costal grooves, but many individuals have 19 and counts of 18 and 21 are also found (Bishop 1943). This variability is also reminiscent of *Plethodon*.

Epaxial musculature (see Fig. 57).- The *dorsalis trunci* is relatively thick and generally similar to that of *Plethodon*. Anterior flexures are relatively long, extending to almost the midpoint of the first vertebra of the pair spanned by the myomere. The more medial part of the anterior flexure is not evident unless the *dorsalis trunci* is displaced laterally. Hyperapophyseal muscles are present beneath the anterior flexures, each being bisected by a thin septum, which arises from one of the horns of the hyperapophysis. Muscle fibers fan from these septa onto the roof of the following vertebra. The more lateral fibers of each hyperapophyseal muscle attach along the medial surface of the deep posterior flexure that is found parallel to it.

A relatively thick superficial layer of fibers extends anterolaterally in the main body of each myomere. Beneath these the other fibers run anteroposteriorly. There is only a slight posterior slant to each myomere, the main bodies rising almost vertically from between the ribs and transverse processes. Deep posterior flexures are, therefore, very long and relatively thin, in order that they reach the posterior zygapophysis to which they insert. The myomeres do not extend laterally beyond the ribs.

Hypaxial musculature (see Fig. 57).- The *subvertebralis* is highly derived, differing markedly from all plethodontids described above, but resembling certain of the bolitoglossines and all of the salamandrid newts. There has been complete loss of the flexures and auxiliary muscles seen previously, the musculature coming to span only a single intervertebral space. The ventral surfaces of the centra and transverse processes are, for the most part, not covered by ventral musculature. The most ventral layer of musculature is composed medially of fibers extending anteroposteriorly between adjacent transverse processes and, more laterally, of fibers running anterolaterally. Each myomere billows ventrally to some degree in the area between each pair of adjacent transverse processes. Tough fascia attaches the posteromedial part of each myomere to a notch in the anteromedial part of the associated ventral rib-bearer. Beneath the ribs each myomere extends a slight distance under the next posterior myomere. This underlapping is somewhat complex, forming a shallow cone-in-cone arrangement.

Presumably correlated with the simplification of the *subvertebralis*, the centra of *B. attenuatus* are modified such that anterior and posterior adjacent cotyles articulate in an oblique manner. That is, the dorsal border of each anterior cotyle is further forward than is the ventral border. This is reflected in the posterior cotyles, so that the centra overlap each other. The centra are apparently fully amphicoelous and basapophyses are absent throughout the column.

Spinal nerves have the same vertebral exits as in other plethodontids. They pass through the *subvertebralis* to a point just distal to the tip of each rib. From here they extend ventrally through the lateral abdominal musculature, in close association with the anterior septum of the myomere that they innervate. They are found between the *transversus* and *o. e. profundus* and are not exposed to the peritoneal cavity.

Lateral abdominal musculature (see Fig. 57).- The lateral abdominal musculature differs little from that of other plethodontines. The *o. e. superficialis* is very thin and relatively narrow, its fibers extending gently posteroventrally and overlapping the *dorsalis trunci* to a significant degree. A small, ill-defined band of muscle fibers extends anteroposteriorly just beneath the horizontal septum, but it is doubtful whether this is deserving of the name *rectus lateralis*. The *o. e. profundus* is as in *Plethodon*.

The *r. a. superficialis* is a thin, broad band composed of two subunits, one on either side of the *linea alba*. Its relationship to the *o. e. profundus* is as in *Plethodon*. The *r. a. profundus* is a small, narrow band extending freely between the *transversus* and *o. e. profundus* and joining the hyobranchium to the pelvic girdle. The posterior point of origin covers a large area, the muscle fanning over most of the ventral surface of the girdle.

The *transversus* is slightly modified away from the basic plethodontine pattern. The fibers extend anteroventrally, but dorsally they curve posteriorly into each subvertebral myomere and under the distal half of each rib to insert on the anterior face of the myoseptum beneath the ribs.

Tribe Bolitoglossini Wake 1966

Bolitoglossa subpalmata (Boulenger 1896)

RANGE. Found in the "high mountains of Costa Rica, above 4,000 feet" (Dunn 1926, p. 390). The genus *Bolitoglossa* is found from "northeastern Mexico to eastern Brazil and central Bolivia" (Wake 1966, p. 53).

HABITAT. Frequents woods and pasture edges, usually under cover. They are apparently sluggish animals (see Dunn 1926, p. 392).

FOSSIL RECORD. None known for the species or the genus.

RELATIONSHIPS. Taylor (1944) classified this species as *Magnadigita subpalmata*, but the genus *Magnadigita* is now included as a junior synonym of *Bolitoglossa*. According to Wake (1966), *Bolitoglossa* is closely related to the other neotropical plethodontids: *Lineatriton*, *Parvimolge*, *Pseudoeurycea*, *Chiropterotriton*, *Thorius*, and *Oedipina*. These were all included in the supergenus *Bolitoglossa*, which Wake believed to be close to *Hydromantes* and, especially, *Batrachoseps*. Relationship of the latter genus to the bolitoglossines is doubtful, but Wake's groupings are similar to those of Tanner (1952) and may be accepted at present. Nevertheless, the suggestion that the bolitoglossines are derived from the hemidactyliines (sensu Wake 1966) is doubtful (see Conclusions).

Hansen and Tanner (1958) considered the long tailed species of *Bolitoglossa* (e.g., *B. platydactyla*, *B. flaviventris*, and *B. mexicana*) to be more primitive and "generalized" than the short tailed species (e.g., *B. rufescens* and *B. occidentalis*).

REMARKS. *B. subpalmata* has a long, relatively robust trunk with 13 costal grooves (= 14 trunk vertebrae) and a long, heavy tail. The limbs are small, but not diminutive, with the hindlimbs somewhat larger than the fore. According to Dunn (1926) there is a high degree of colour variability, perhaps correlating with habitat diversity.

Epaxial musculature (see Fig. 58).- The *dorsalis trunci* is like that in the plethodontines. The myomeres are anteroposteriorly elongate and, correlated with the short ribs, relatively narrow transversely. The anterior flexures are extremely small, each apex giving rise to a forwardly projecting septum that parallels the associated hyperapophyseal muscles ventrally. Muscle fibers extend anteroposteriorly in the myomeres.

Medially, a thin layer of anteroposterior fibers overlies the hyperapophyseal muscles, which are relatively large, but otherwise as in other plethodontids. A broad, very short flexure extends posteriorly from the posteromedial surface of the main body of each myomere to attach to the posterior zygapophysis of the second vertebra of the pair spanned by that myomere. The posterior flexures of plethodontids described previously are much longer.

Hypaxial musculature (see Fig. 58).- The *subvertebralis* is similar to that of *Plethodon*, *Ensatina*, and *Hemidactylium*, but differs from that of *Batrachoseps*. Laterally, beneath adjacent ribs, each myomere inclines anteriorly to some degree, underlapping its forward neighbour. A short, broad posterior flexure is associated with each transverse process. The apex of each flexure does not quite reach the posterior cotyle of the vertebra with which it is associated. Muscle fibers run posteromedially from the internal surface of each septum to attach to the lateral edge of the cotyle, and also fan posteriorly into the body of the following posterior flexure. The septa and their associated muscle fibers cannot be termed posterior basapophyseal muscles as they are not directly associated with the posterior basapophyseal region of the cotyle, but with the myomeres and transverse processes. In this feature *Bolitoglossa* is more primitive than any of the euryciines described below, indicating derivation of the two groups from separate ancestry within the Plethodontini. Hansen and Tanner (1958) describe and figure elongate posterior basapophyses in some species of the genus. One might expect that the posterior flexures are more intimately associated with the centra in these species.

Spinal nerve patterns do not differ significantly from those described above for the plethodontines (see also Edwards 1976).

Lateral abdominal musculature (see Fig. 58).- Excepting the slight overlap of the *dorsalis trunci* by the *o. e. superficialis*, the lateral abdominal musculature of this species is as in adult *Ensatina*.

Pseudoeurycea cephalica (Cope 1865)

RANGE. Found in the mountains of southcentral Mexico (Dunn 1926). The genus is found from "Nuevo Leon and Tamaulipas in northeastern and Nayarit in western Mexico to Guatemala" (Wake 1966, p. 54).

HABITAT. Individuals are "much like *Plethodon glutinosus* in their habitat . . . coming from the ground, under bark of rotten logs, [or] under chips and débris on the ground" (Dunn 1926, p. 381).

FOSSIL RECORD. None known for the species or the genus.

RELATIONSHIPS. Dunn (1926) grouped all species of free-tongued Central and South American plethodontids in the genus *Oedipus*. He suggested that *Oedipus bellii* (= *Pseudoeurycea bellii*) was perhaps the most primitive *Oedipus* (= the supergenus *Bolitoglossa*, see Wake 1966). Taylor (1944) erected the genus *Pseudoeurycea* to include several of those species classified previously in *Oedipus*. Tanner (1952) allied *Pseudoeurycea* with *Chiropterotriton*, a suggestion followed by Wake (1966).

Baird (1951) divided *Pseudoeurycea* into four species groups: the *gadovii* group (*P. gadovii*, *P. unguidentis*, and *P. smithi*), the *leprosa* group (*P. leprosa*, *P. rex*, *P. goebeli*, *P. cochranae*, and *P.*

robertsi), the *bellii* group (*P. gigantea*, the largest living plethodontid, and *P. bellii*), and the monotypic *cephalica* group. Baird considered the *bellii* group to be the most primitive on the following criteria:

1) lack of well-marked sexual dimorphism;
2) cartilaginous remnants of the last pair of ribs, and
3) internasal gland and the associated intervomerine foramen small.

REMARKS. *P. cephalica* is relatively large with a robust, *Plethodon*-like trunk and a rounded, tapering tail, which is not greatly elongate. There are 14 presacral vertebrae (a number constant throughout the genus according to Wake 1966) and 13 costal grooves. The trunk vertebrae appear to be structurally amphicoelous, but the anterior cotyles are of lesser diameter than the posterior and fit into them.

The limbs are small, but not diminutive. Toes are webbed basally and stubby. Sexual dimorphism is evident in that males have enlarged, overhanging upper lips and a distinct submental gland.

Epaxial musculature (see Fig. 59).- The *dorsalis trunci* is thick, but not expanded. The medial portion of each anterior flexure appears to have been eliminated, so that there is no fanning of the muscle fibers within the flexures. Fibers tend to extend anteroposteriorly in the myomeres, although there is a very slight anterolateral component in the main body of each myomere. The myomeres incline posteriorly at a relatively sharp angle, in contrast to their gentle inclination in *Bolitoglossa*. The ribs do not extend all the way to the lateral edge of the *dorsalis trunci*.

Deep posterior flexures are present throughout the trunk. These arise on the internal edge of the main body of each myomere and extend posteromedially. The flexures are tapered and insert on the neural arches anterodorsal to the posterior zygapophyses. Hyperapophyseal muscles appear to lack long septa and the hyperapophyses resemble those of *Bolitoglossa*, but are relatively larger.

Hypaxial musculature (see Fig. 59).- The *subvertebralis* is very like that of *Bolitoglossa*, but with several distinctions. Posterior flexures extend further laterally and posteriorly. The septum extending back from each flexure is long and gives rise to muscle fibers that fan posteriorly to form the body of the following posterior flexure. The main body of each myomere inclines anteriorly. The ventral fibers extend anterolaterally, but the more dorsal align posterolaterally between adjacent ribs. At the cartilaginous joint between each ventral rib-bearer and the ventral arm of the associated rib a small septum arises. This extends a short distance posteriorly and serves as a site of insertion for several of the intercostal muscle fibers.

The spinal nerves are patterned as in *Bolitoglossa*.

Lateral abdominal musculature (see Fig. 59).- The structure and relationships of the *r. a. profundus*, *r. a. superficialis*, and *o. e. superficialis* conform to the pattern seen in *Bolitoglossa subpalmata*, but significant modification of the *transversus* and *o. e. profundus* is evident. This involves the dorsal parts of the latter two layers, just ventral to the horizontal septum. Anteriorly in each muscle segment, part of the *transversus* has come to lie external to the *o. e. profundus* and attaches to the horizontal septum. The two layers have thus reversed their positions in the anterior part of each myomere, but the functional significance of this is obscure.

Chiropterotriton Taylor 1944

RANGE. This genus is found from "southern Nuevo Leon and southwestern Tamaulipas through eastern and east-central Mexico to Guatemala, El Salvador, Honduras, and Costa Rica" (Wake 1966, p. 54).

HABITAT. These are "small mountain salamanders [with species] adapted to both terrestrial and arboreal life" (Taylor 1944, p. 213).

FOSSIL RECORD. None known.

RELATIONSHIPS. Basing his conclusions on the structure of the hyobranchial musculature, Tanner (1952) allied *Chiropterotriton* with *Pseudoeurycea*. *Parvimolge* and *Lineatriton* were suggested to be close to these two genera. Wake (1966) followed Tanner and grouped *Chiropterotriton* with the other neotropical plethodontines in the supergenus *Bolitoglossa*.

REMARKS. Three species of *Chiropterotriton* were available for study: the terrestrial *C. chiroptera* (Cope 1863) and *C. chondrostega* (Taylor 1941), and the bromeliad-dwelling *C. xolocalcae* (Taylor 1941). According to Taylor (1944, p. 216) *C. chiroptera* is most numerous at high elevations, being found "deep among rock piles, in the roots of rotting stumps and sometimes in the thick basal masses of the mountain grass clumps, which remain moist during much of the dry season." Dunn (1926, p. 371) referred to *Oedipus chiropterus* as a subalpine species inhabiting pine forests. Its habits are "much like those of *Plethodon cinereus* and . . . [it is] found among decaying vegetable débris on the floor of the forest, under logs, beneath the bark of dead logs, and under any loose material."

The tail in *C. chiroptera* is relatively long and the trunk is thin but not attenuate. There are generally 13 costal grooves present and Wake (1966) states that there are 14 trunk vertebrae in all species of *Chiropterotriton*. The limbs are small, the toes hardly webbed and quite stubby. In preserved specimens of all three species, the trunk vertebrae are aligned at slight angles to each other. That is, one vertebra will extend anterolaterally to the left, the next anterolaterally to the right, the next to the left, and so on. Only *C. chiroptera* has been figured.

Epaxial musculature (see Fig. 60).- The *dorsalis trunci* of *Chiropterotriton* differs somewhat from that of *Pseudoeurycea*. The anterior flexures are short and provided with anteriorly directed, relatively elongate septa. In this they are like *Bolitoglossa*. The myomeres rise posterodorsally at a greater angle than in the latter genus, resembling *Pseudoeurycea* more closely in this regard. Prominent deep posterior flexures are developed along the column, also as in *Pseudoeurycea*. Hyperapophyseal muscles resemble those of *Bolitoglossa* in their long septa. Muscle fibers in the main bodies of the myomeres extend anteroposteriorly.

Hypaxial musculature (see Fig. 60).- In *C. chiroptera* the *subvertebralis* is developed as in *Batrachoseps attenuatus*, with the loss of posterior flexures. Differences in the development of this unit between the two indicate the resemblances to be convergent, however (see also Fig. 57). In the anterior part of the trunk is a slight posterior extension of the myomeres medially, but this does not form a posterior flexure. In the posterior third of the trunk the myomeres are limited solely to the area between two adjacent tranverse processes and their ribs. The ventralmost fibers extend anteroposteriorly, those further dorsal run posterolaterally. The structure of the *subvertebralis* is markedly different from that of *Pseudoeurycea cephalica*, but there is resemblance in the common possession of posteriorly directed septa in the intercostal musculature.

In *C. chondrostega*, also a terrestrial species, the *subvertebralis* has the same structure as that of *C. chiroptera*. In contrast to these species, the bromeliad-dwelling *C. xolocalcae* has fully developed posterior flexures, each with a posteriorly directed septum from which muscle fibers fan posteriorly. The apex of each posterior flexure extends to the border of the posterior cotyle of the adjacent vertebra. The correlation between the simplified *subvertebralis* and terrestrial habits (*Batrachoseps attenuatus* is also terrestrial) is of note. Nevertheless, the presence in a single genus of two quite different kinds of subvertebral pattern indicates that all species of the Neotropical genera will have to be studied before concrete phylogenetic and functional interpretations can be made. At present, generic phylogenies for the bolitoglossines are very uncertain.

In all three species the spinal nerves of the trunk exit intravertebrally and extend laterally and then posteriorly much as in *Pseudoeurycea*.

Lateral abdominal musculature (see Fig. 60).- The lateral abdominal musculature of *C. chiroptera* differs from that of *Pseudoeurycea cephalica* in that it lacks the modifications of the *transversus* and *o. e. profundus* seen in the latter. In *C. chiroptera* the *transversus* extends medially to insert on the anterior faces of the ribs, but there is no interdigitation with the *o. e. profundus*. The *r. a. profundus* is relatively narrower than that of *P. cephalica*. Midventrally, the two halves of the *r. a. superficialis* are separated by a wide band of connective tissue. Otherwise the situation in the two species is similar.

The more arboreal *C. xolocalcae* has similarly developed lateral abdominal musculature, whereas the terrestrial *C. chondrostega* differs in resembling *Pseudoeurycea cephalica* with respect to the relationship of the *transversus* and *o. e. profundus*. There appears to have been a notable amount of mosaic evolution within the trunk musculature of *Chiropterotriton* and it is likely that similar situations will become evident in other Neotropical genera. This indicates that drawing detailed generic phylogenies for the Bolitoglossini is probably an illusory exercise at present. Parallelisms and convergence are undoubtedly very common in this group and it will prove difficult to work out real relationships.

Hydromantes brunus Gorman 1954

RANGE. Only three isolated populations in the Yosemite Valley in the County of Mariposa in California are known, all within an area of one and a half miles (Gorman 1954, 1964).

HABITAT. *H. brunus* is found in limestone areas between 1,285 and 2,500 feet elevation, associated with Chaparral plants of the Upper Sonoran life-zone. It is associated with "*Aneides lugubris*, *Batrachoseps attenuatus* . . ., *Taricha torosa*, and *Rana boylei*. The first two species occur with *Hydromantes brunus*, often being found at the same time under the same rock" (Gorman 1954, p. 157). Reproduction is oviparous (Gorman 1956).

FOSSIL RECORD. None known for the species or the genus.

RELATIONSHIPS. Other species of *Hydromantes* are *H. shastae* and *H. platycephalus*, also from California, and *H. genei* and *H. italicus* from Europe. The former is on the Island of Sardinia and the latter is known from the Maritime Alps and Apennines (Gorman 1964). The generic distribution is highly disjunct, probably owing to invasion of the Old World and not relictual.

Dunn (1926, p. 31) considered *Hydromantes* to share a common ancestor with *Gyrinophilus* and that there was "no alliance between *Hydromantes* and *Oedipus* [= supergenus *Bolitoglossa*] except the common origin of the two from some terrestrial stock." Piatt (1935) believed *Hydromantes* to be most closely related to "*Oedipus*," and these along with *Batrachoseps* to be closest to the *Plethodon* group. Taylor (1952) held that the genus was closely related to *Bolitoglossa* and the other Neotropical plethodontids. Wake (1966) indicated *Hydromantes* to be closest to the supergenus *Bolitoglossa* and *Batrachoseps*, but with the latter two taxa being closer to each other than either is to *Hydromantes*. He stated (p. 69) that "*Hydromantes* is the most generalized [?primitive] of the three supergenera." Nevertheless, the absence of the free tongue in *Batrachoseps* and its presence in *Hydromantes* and the supergenus *Bolitoglossa* would seem to contradict Wake's interpretation. I classify *Hydromantes* as a member of the Bolitoglossini, along with *Bolitoglossa* and its allies.

REMARKS. *H. brunus* differs from the other North American species of *Hydromantes* in its larger size, coloration, and in proportional differences of the head, body, tail, and eyes. Palatal teeth also have a differing pattern (Gorman 1954). There are 13 costal grooves, which correlate with 14 trunk vertebrae. The premaxillae are separate and prefrontals are lacking (see Wake 1966). The tongue is free.

Epaxial musculature.- The *dorsalis trunci* is extremely thin, with only a few layers of muscle fibers overlaying the vertebrae and ribs. In some ways it resembles certain of the more derived salamandrid newts. Anterior flexures are relatively short, but their apparent length is increased owing to the extreme overlap of the main bodies of the myomeres. The anterior flexures are each provided with a forwardly directed septum, from which muscle fibers fan anteriorly. Owing to the thinness of the *dorsalis trunci*, the hyperapophyseal muscles are closely associated with the anterior flexures. They are not ventral to the flexures, but occur slightly ventromedial to them. Muscle fibers extend from each hyperapophyseal septum to an anterior flexure.

The main bodies of the myomeres do not extend laterally beyond the ribs. The ribs end in enlarged cartilaginous caps, which are barely covered by the *dorsalis trunci*. Owing to the marked overlap of, and the small mass of musculature in, the myomeres, they resemble a series of overlapping disks. Deep posterior flexures are absent.

Hypaxial musculature.- The *subvertebralis* is very thin and does not extend onto the ventral surfaces of the centra. Posterior flexures are short, extending only a slight distance posterior to their respective transverse processes. The medial septum of each flexure extends anteromedially to the intercentral joint between its vertebra and the latter's next anterior neighbour. This septum does not associate with the posterior cotyle but with the joint, and posterior basapophyses are correspondingly absent. Each posterior flexure has a short septum extending backwards, from which muscle fibers fan.

The fibers beneath the ribs extend anteriorly and very slightly laterally. Those between the ribs run posterolaterally and are continuous with the *o. e. profundus* distally.

The patterns of the spinal nerves are as in other bolitoglossines described here, with a relatively long subvertebral exposure to the peritoneal cavity.

Lateral abdominal musculature.- The muscle layers of the lateral wall of the body are very narrow, correlating with the increased width of the *rectus abdominis*. The *o. e. superficialis* is narrow and does not extend dorsally far enough to meet the *dorsalis trunci*, although a few fibers overlap the latter complex in the more anterior region of the trunk. It does, however, slightly overlap the *rectus abdominis* ventrally. Muscle fibers extend posteroventrally at an angle slightly offset from the horizontal, which contrasts with the vertical alignment in the *o. e. superficialis* of the other bolitoglossines dissected.

The *o. e. profundus* has fibers oriented at the same angle as those of the *o. e. superficialis* and is likewise segmented by myocommata.

It blends partially with the intercostal musculature dorsally and is overlapped externally by a short, thin flap of the *r. a. superficialis*, with which it also blends. The *transversus* originates dorsally along the anterior edges of the subvertebral myosepta and its fibers extend anteroventrally. This sort of origin produces a step-like dorsal edge to the *transversus*. The unit is not segmented and proceeds ventrally along the internal surface of the *o. e. profundus* and then the *r. a. profundus* to meet the *r. a. superficialis*. Although notably wider, the *r. a. superficialis* is developed as in other bolitoglossines. Perhaps surprisingly in light of the markedly protrusive tongue, the *r. a. profundus* does not appear to be free within the body wall.

b) Subfamily Desmognathinae Boulenger 1882
Tribe Euryciini Wake and Lombard 1973
Eurycea bislineata (Green 1818)

RANGE. This is the most wide-ranging species of *Eurycea*, being found "from southeastern Canada to Florida, and west to the Mississippi and into eastern Illinois" (Mittleman 1966, p. 45.1).

HABITAT. "This is essentially a species of the brooksides, where it hides beneath stones and logs in the well saturated soil. It is at home in the water . . . and swims freely . . . . Occasionally found in drier situations some distance from water" (Bishop 1943, p. 404). Eggs are laid in streams and the larvae are aquatic from time of hatching. There is at least one confirmed instance of a female guarding the eggs (Salthe and Mecham 1974).

FOSSIL RECORD. None for the species or the genus.

RELATIONSHIPS. Dunn (1926) believed *Eurycea* to be derived with respect to *Gyrinophilus* and to be allied to *Stereochilus* and *Typhlotriton*. Along with *E. multiplacata*, *E. bislineata* was considered to be the most primitive species of the genus. Dunn included all free-tongued plethodontids and their allies in his *Eurycea* generic group. Piatt (1935) derived *Eurycea* from *Pseudotriton*, which was in turn derived from *Gyrinophilus*, but he considered the free-tongued plethodontids to be diphyletic. In contrast to these workers, Noble (1931) noted that *Eurycea* was in some ways more primitive than *Gyrinophilus*.

Wake (1966) considered *Eurycea* as most closely related to *Typhlotriton*, *Haideotriton*, and *Typhlomolge*, and that these four genera were derived from *Gyrinophilus-Pseudotriton* stock. In overall structure *Eurycea* is no more derived than *Gyrinophilus*, however, and in terms of the *subvertebralis* it is, perhaps, somewhat more primitive. In the case of *Eurycea* and its allies it is not particularly profitable to draw detailed generic phylogenies, as there is simply not enough evidence to make hypotheses concrete. I further differ from Wake as regards the relationships of *Hemidactylium*. This genus is not particularly close to *Eurycea*, or to any other of Wake's Hemidactyliini. I therefore recognize a tribe Euryciini, which is equivalent to the Hemidactyliini, but without *Hemidactylium* (see Conclusions).

REMARKS. *E. bislineata* has a long, thin body with 14 costal grooves and an elongate, tapering tail. The limbs are small, but not greatly disproportionate. The trunk musculature is thick, but not massive. *E. junaluska* was also available for study, but did not differ from *E. bislineata* in terms of the trunk musculature.

Epaxial musculature (see Fig. 61).- The epaxial musculature is very similar to that of other members of the *Eurycea* group. Each myomere rises steeply posteriorly from between adjacent ribs. The anterior flexures are short and overlap each other minimally. Relatively large deep posterior flexures extend posteromedially from the main body of each myomere to insert anterior to the hyperapophysis of the next posterior vertebra. Hyperapophyseal muscles are of typical plethodontid development. The muscle fibers in the main body of each myomere extend anteroposteriorly, although the most superficial layer shows slight anteroventral alignment.

Hypaxial musculature (see Fig. 61).- The *subvertebralis* is directly comparable to that of the plethodontines, but the posterior flexures have been modified to what may be termed true posterior basapophyseal muscles. Medially the presence of posterior basapophyseal muscles is largely obscured by longitudinal muscle fibers, which underlie this complex. Above these, each vertebra has a pair of relatively thin posterior basapophyseal muscles. These are homologous to the posterior flexures of *Plethodon* and its allies, being produced by medial migration of the flexures and closer association with the vertebrae. Posterior basapophyses are present on the more anterior trunk vertebrae (T1 through T6 or T7) and on the atlas. Posterior basapophyseal septa attach to these processes and muscle fibers fan posteriorly from the septa. The attachment of these fibers to the centrum and transverse process on either side of the following vertebra forms the origin of each posterior basapophyseal muscle.

Based on positional relationships, the posterior basapophyseal septa are homologous to the single septa that extend posteriorly from the posterior flexures in plethodontines (*Gyrinophilus* perhaps shows this relationship more clearly, see Fig. 65). A septum extends posteromedially from a point just below the distal end of each ventral rib-bearer and joins to the posterolateral edge of the centrum of the same vertebra. Muscle fibers run posterolaterally from the basapophyseal septum to the septum just described, which is homologous to the external septum of the posterior flexure in plethodontines (q.v.). Although *Aneides lugubris* has a similar sort of arrangement to that described, there are certain differences and the posterior basapophyseal muscles in it are probably convergent upon the condition in euryciines. The true posterior basapophyseal muscle represents a shared and derived character serving to unite *Eurycea* and its allies with *Desmognathus*, *Leurognathus*, and *Phaeognathus*. It is also evidence against relationship of bolitoglossines and euryciines.

The main body of each myomere, distal to the transverse processes, extends a short distance past the ends of the ribs. The more ventral fibers next to the peritoneum extend anterolaterally. In contrast to some other members of the Euryciini, this layer is relatively thick and not overshadowed by the more dorsal fibers, which run anteroposteriorly. The latter fibers are largely limited to the area immediately between adjacent transverse processes. Dorsal to the anterolateral fibers, but still slightly ventral to the ribs, is a layer that runs posterolaterally. This group continues dorsally to become the intercostal group, and laterally and ventrally to form the *o. e. profundus*. The main bodies of the myomeres drop ventrally and posteriorly, especially at the more lateral border of the *subvertebralis*.

Each spinal nerve in the trunk region exits intravertebrally from a small hole in the wall of the neural arch. The nerve then proceeds posterolaterally through the myomere, paralleling the ribs. At the lateral edge of the subvertebral portion of the myomere the spinal nerve extends between the *transversus* and *o. e. profundus*. The spinal nerve is not exposed to the peritoneum.

Lateral abdominal musculature (see Fig. 61).- The external *o. e. superficialis* spans the area between the epaxial musculature and the *rectus abdominis*, overlapping each slightly. The fibers of the *o. e. superficialis* are aligned parallel to the segmenting myocommata, but owing to posteroventral declination of the myocommata the fibers are aligned posteroventrally with respect to the trunk. The thicker *o. e. profundus* lies deep to this layer, being a direct continuation of the intercostal musculature. Its fibers extend posteroventrally between adjacent myocommata at an angle just slightly displaced from the horizontal. Ventrally the *o. e. profundus* blends with the *r. a. superficialis*, but the latter has a thin flap that overlaps the former externally.

The *transversus* is deep to the *o. e. profundus* and there is no *o. internus*. The *transversus* is not divided by myocommata, is relatively thick, and the fibers extend anteroventrally. It extends a short way into the *subvertebralis*, but is not connected to the ribs. Ventrally it underlaps the *r. a. profundus* and meets the *r. a. superficialis*. The *rectus abdominis* is developed as in other plethodontids.

Alignment of the myocommata of the lateral abdominal series differs from that of other plethodontids. The septa extend posteroventrally at a slight angle away from the vertical. Then, at the level of the transition between the *o. e. profundus* and *r. a. superficialis*, they change direction and proceed anteromedially to the centre line of the belly.

Eurycea quadridigitata (Holbrook 1842)

RANGE. This salamander is found from "North Carolina south to middle Florida, west through [the] Gulf States to [western] Texas . . . [and] northward to Arkansas and Oklahoma" (Bishop 1943, p. 446).

HABITAT. According to Bishop (1943, p. 446) the species is "most abundant in low, swampy places, beneath logs, bark, and other surface rubbish, in leaf-filled trickles from springs, and in the debris along the margins of pools in river swamps and marshes . . . . [It is] mainly terrestrial in summer and fall, but enters the water for . . . egg-laying . . . in December." There is no guarding of the eggs (Salthe and Mecham 1974).

FOSSIL RECORD. None known.

RELATIONSHIPS. Wake (1966) included this species in the genus *Eurycea*, noting that the only good distinguishing character separating it from the other species is the presence of four toes on the hind feet. Mittleman (1967, p. 44.1), however, considered separate generic status justified, stating that *Manculus quadridigitatus* "differs from all *Eurycea*; and all plethodontids except *Hemidactylium* and *Stereochilus*, in that the tail fin of the larva extends onto the body." He also stated (p. 44.1) "that the differences which set apart *Manculus* from *Eurycea*, though quantitatively few are highly significant and may be interpreted as those of a relict species derived from a pre-*Eurycea* progenitor, the similarities between *Manculus* and *Eurycea* being a result of generic convergence."

Piatt (1935) and Wake (1966) argued that "*Manculus*" is a derivative of *Eurycea*, and Dunn (1926) included *E. quadridigitata* in the genus *Eurycea*. I cannot agree that the absence of a single toe and a somewhat elongated tail fin are "highly significant" features. Study of the trunk musculature and comparison with that of *E. bislineata* and *E. junaluska*, as well as other plethodontids, confirms the usage of Dunn (1926) and Wake (1966). It is more probable, as suggested by Wake (1966), that *E. quadridigitata* is of common origin with the other species of *Eurycea*.

REMARKS. The form of the body of this salamander is like that of *E. bislineata*.

Epaxial musculature (see Fig. 62).- The *dorsalis trunci* is quite similar to that of *E. bislineata*, but with several distinctions. The anterior flexures are somewhat longer than those of *E. bislineata*, presumably in correlation with the larger hyperapophyses. As in *E. bislineata*, the anterior flexures change along the column. In the area of the pectoral girdle the myomeres extend anteriorly, but a flexure is lacking. This may correlate with the absence of hyperapophyseal spines in the anterior region of the trunk. Anterior flexures are some three times as long as those of *E. bislineata*, seemingly a more primitive condition (compare other euryciines below).

The main bodies of the myomeres rise more steeply than is the case in *E. bislineata*. The fibers are deflected anterolaterally and anteroventrally. This alignment holds true deep into the myomeres, whereas in *E. bislineata* the deep fibers extend anteroposteriorly. As in the latter species, deep posterior flexures and hyperapophyseal muscles are developed.

Hypaxial musculature (see Fig. 62).- The *subvertebralis* differs somewhat from that of *E. bislineata*. In ventral view the presence of posterior basapophyseal muscles is evident without the removal of any muscle fibers. There is a more or less distinct division of the *subvertebralis* into the basapophyseal unit and the lateral subcostal portion. Posterior basapophyseal muscles are developed as in *E. bislineata*, but are more readily distinguishable.

Muscle fibers within the main parts of the myomeres are aligned as in *E. bislineata*, but there is an apparent difference in the orientation of the myomeres themselves. In *E. bislineata* each myomere descends posteroventrally from between adjacent ribs with little variation along the column. In *E. quadridigitata*, however, there is change along the column. In the anterior part of the column, next to the pectoral girdle, the myomeres tilt posteriorly. In the midtrunk region they descend more or less straight ventrally, whereas in the more posterior regions the distal parts of the myomeres are inclined anteriorly. How much of this difference reflects the effects of preservatives is uncertain owing to small sample size.

The spinal nerves are developed as in *E. bislineata*.

Lateral abdominal musculature (see Fig. 62).- Except as noted, the lateral abdominal musculature is as in *E. bislineata*. The myosepta extend straight ventrally from the epaxial myomeres, with no posterior deflection. Beneath the *o. e. superficialis* the myocommata segmenting the *r. a. superficialis* extend anteromedially for a short distance and then bend posteromedially. The *o. e. profundus* blends completely with the *r. a. superficialis* and the latter does not overlap the former externally.

Typhlotriton spelaeus Stejneger 1893

RANGE. "This salamander is restricted to [limestone] caves and springs on the Salem and Springfield plateaus of the Ozark region of Arkansas, Kansas, Missouri, and Oklahoma" (Brandon 1970c, p. 84.1).

HABITAT. Metamorphosed individuals are restricted to caves and "are more terrestrial than other true cave salamanders. The larvae are found in springs and streams, both in the open and in caves" (Bishop 1943, p. 351). Adults are found both in the water and on the walls of caves (Dunn 1926). Breeding behavior is unknown.

FOSSIL RECORD. None known.

RELATIONSHIPS. Stejneger (1892) classified this monotypic genus in the Desmognathidae on the basis of its opisthocoelous vertebrae. Dunn (1926, p. 251) believed it to be derived from an ancestor "very close to the ancestors of the *Eurycea* group if not from the same stock." He noted similarities in the vertebrae, degree of sexual dimorphism, larval structure, and cranium to *Pseudotriton*. Noble (1931) also considered *Typhlotriton* to be related to *Eurycea*, and to be possibly ancestral to *Typhlomolge*. Piatt (1935) suggested that *Typhlotriton* was close to *Gyrinophilus*, *Pseudotriton*, and *Eurycea* and that it gave rise to *Typhlomolge*. Wake (1966) produced a more specific ancestor, deriving the genus from a common stock shared with *Eurycea* and *Haidetriton*.

The *dorsalis trunci* is more derived than that of *Eurycea*, whereas the structure of the *subvertebralis* appears more primitive. This may simply reflect paedomorphosis, however, and *Typhlotriton* is close to *Eurycea*, as suggested by previous workers.

REMARKS. These are normally proportioned, blind salamanders. The skin is only slightly pigmented, with a white or flesh-coloured base and small orange or black spotting dorsally (Dunn 1926, Bishop 1943). There are 16 costal grooves, the trunk being relatively robust and not elongate. The tail is relatively long, robust, and rounded in cross-section. The limbs are robust, not spindly as in *Typhlomolge*. The head is depressed, narrow, and quite elongate.

Epaxial musculature (see Fig. 63).- The *dorsalis trunci* is of the same basic plan as other members of the Euryciini. Anterior flexures are V-shaped anteriorly, with only a small part buried medially (contrast *Gyrinophilus*, Fig. 65). They are more or less confluent with the hyperapophyseal muscles ventrally.

The deep posterior flexures are large and well developed, each inserting on the anterior face of one side of a hyperapophysis. These flexures receive some of the fibers from the paralleling hyperapophyseal muscles. The main bodies of the myomeres are large, rising steeply from between adjacent ribs. The ribs do not extend to the edge of the *dorsalis trunci*, although they are long. Superficial fibers on the myomeres extend anteroposteriorly, whereas the deeper ones run anterolaterally and anteroventrally. The *dorsalis trunci* is covered by tough fascia, to which is attached the *o. e. superficialis* on either side.

Hypaxial musculature (see Fig. 63).- The *subvertebralis* shows resemblances to that of *Eurycea*, but also recalls *Gyrinophilus* to some extent. There are distinct, relatively short posterior flexures extending back from each transverse process. These do not reach the posterior cotyle of the associated vertebra. Each flexure gives rise to a long, strap-like septum, which extends posteriorly. These do not insert onto basapophyses, but are associated with the posterior flexures. Fibers fan posteriorly from these septa, forming the bodies of the following posterior flexures. Each flexure is partially underlapped by fibers of the following myomere. That is, it extends into the following myomere, a feature resembling the condition in *Gyrinophilus*. In the lack of association of the posterior septum to the posterior basapophyseal region the species recalls the plethodontines.

Subcostally, the main parts of the myomeres extend straight ventrally, excepting a slight anteroventral twist most distally. The muscle fibers are here arranged into two series: the more ventral extend anterolaterally, the more dorsal intercostals run posteroventrally. This situation is as in the other members of the Eurycliini. The subvertebral parts of the myomere extend only a very short distance beyond the tips of the ribs.

The exits and pathways of the spinal nerves are of typical plethodontid pattern. However, there is a greater peritoneal exposure of the nerves than is seen in other euryciines, although *Stereochilus* closely approaches *Typhlotriton*.

Lateral abdominal musculature (see Fig. 63).- This part of the trunk musculature is like that of other euryciines and needs little description. The *r. a. profundus* is quite wide and there is, perhaps, some increase in the size of the *rectus lateralis*. Myosepta extend a short distance into the *transversus* at its dorsal edge, which is not a general plethodontid feature.

Stereochilus marginatus (Hallowell 1856)

RANGE. The monotypic *Stereochilus* is found on the Atlantic coastal plain from southern Virginia and then southward into Georgia (Bishop 1943).

HABITAT. Although sometimes found on land under cover in damp areas, the species is primarily aquatic. "They are perhaps most abundant in pools and slow streams in swampy [cypress] woods," often in leaf debris (Bishop 1943, p. 346). The larvae are aquatic, eggs being laid in or near water (Rabb 1966), and guarded by the female (Salthe and Mecham 1974).

FOSSIL RECORD. None known.

RELATIONSHIPS. As noted by Dunn (1926, p. 247), "in many points it reminds one of *Pseudotriton*, though, of course neither could conceivably be ancestral to the other, while it has points of similarity with *Typhlotriton* as well. But certainly none of the features . . . call to mind any other genus of *Plethodontidae* [sic] . . . It simply shows general affinities to the more primitive members of the *Eurycea* group." Piatt (1935) considered *Stereochilus* to be an early derivative from the *Eurycea* group.

Wake (1966) followed this general scheme, believing *Stereochilus* to be an early offshoot of the Euryciini (his Hemidactyliini). According to Wake (p. 63), "One of the most primitive characters of *Stereochilus* is the presence in adults of a distinct . . . lateral line system on the heads." Of course, this feature is not primitive, being simply owing to retention of larval characteristics in the adult and, therefore, derived. In spite of this misinterpretation, *Stereochilus* is in many respects primitive within the Euryciini. Whether or not the lack of a free tongue is primitive (as the schemes of Piatt 1935 and Wake 1966 indicate) or derived remains uncertain. The fixed tongue of *Stereochilus* may well be a secondary paedomorphic trait (see Conclusions).

REMARKS. These are relatively small, slender salamanders with short limbs and a short, low, and laterally compressed tail. The trunk is robust, but elongated, and the head is relatively small and flattened. Dunn (1926) cites costal groove counts of 18 and 19.

Epaxial musculature (see Fig. 64).- The *dorsalis trunci* is massive, deeply burying the vertebral column. The main bodies of the myomeres rise posterodorsally at a steep angle. The muscle fibers within these blocks extend anterolaterally between the myosepta. Large deep posterior flexures are present throughout the column. These extend posteromedially from each myomere into the following myomere to insert onto one side of the hyperapophysis of the following vertebra. The posterior flexures also serve as sites of attachment for some of the fibers from the hyperapophyseal muscle fibers.

Anterior flexures extend further forward than is the case in either *Gyrinophilus* or *Pseudotriton*. A small portion of the inner part of each flexure (in which fibers extend anteromedially) is visible in dorsal view, but the majority of this part is buried owing to ventral deflection. The ventral portions of the anterior flexures appear to be confluent with the hyperapophyseal muscles. These latter are developed as in other plethodontids.

Hypaxial musculature (see Fig. 64).- The basic structure of the *subvertebralis* is very similar to that in *Gyrinophilus* and *Pseudotriton* although differing in details of the orientations of muscle fibers and development of septa. There are two layers in the massive, anteroventrally inclined main body of each subvertebral myomere. The ventral unit is composed of fibers extending anterolaterally, the dorsal layer has its fibers running posterolaterally. A seemingly unique muscle block is partially differentiated within the intercostal series. This has a narrow point of attachment on the distal end of each transverse process and fans posteriorly to attach to the anterior face of the following transverse process and proximal part of the associated rib.

As in *Gyrinophilus* and *Pseudotriton*, posterior flexures are present next to the centra. There is, however, less intimate association with the centra, and the posterior flexures cannot be said to represent true posterior basapophyseal muscles. Nevertheless, they differ from the posterior flexures seen in the Plethodontinae. From the posterior end of each flexure a long, strap-like septum proceeds backwards. This septum gives rise to fibers that extend posteriorly with medial, lateral, dorsal, and ventral components to form the body of the next posterior flexure. The centra are opisthocoelous, in correlation with the direct pull exerted on the posterior of each centrum (see Conclusions).

Spinal nerves exit from the column as in other plethodontids. They are exposed to the peritoneum for a short distance and then extend external to the *transversus* (compare *Gyrinophilus*, Fig. 65 and *Pseudotriton*, Fig. 66).

Lateral abdominal musculature (see Fig. 64).- The structure of this unit shows the greatest resemblance to that of *Pseudotriton*, but differs in the following:

1) *o. e. superficialis* not as wide and with fibers oriented in the vertical plane;
2) *rectus lateralis* somewhat larger and more differentiated;
3) *r. a. profundus* narrower and less separate from the *r. a. superficialis*;
4) *r. a. superficialis* much wider;
5) myocommata extending a shorter distance into the *transversus*.

These distinctions probably reflect paedomorphosis in *Stereochilus*, or at least adaptation to a more highly aquatic environment. *Stereochilus* differs from *Gyrinophilus*, but is more similar to *Pseudotriton*, in that the spinal nerves follow the myocommata through the lateral abdominal musculature, and in not having the *transversus* inserted on the distal ends of the ribs.

Gyrinophilus porphyriticus (Green 1827)

RANGE. "The Appalachian uplift of the eastern United States and adjacent Canada, northward to western Maine and southern Quebec, westward into areas adjoining the Appalachian uplift from Cincinnati, Ohio, northeastern Mississippi, and southward to the Fall Line in Alabama, but not quite to the Fall Line in South Carolina and Georgia" (Brandon 1967, p. 33.1).

HABITAT. The exact ecological requirements are uncertain, but it is "most often encountered in or along small, clear, upland streams, in clear springs, and in caves" (Brandon 1967, p. 33.1). "Also likely to be found in any wet depression beneath logs, stones, or leaves in the surrounding forests" (Conant 1958, p. 242). The eggs are guarded (Salthe and Mecham 1974).

FOSSIL RECORD. None known for the species or the genus.

RELATIONSHIPS. The genus is generally considered "the most primitive of the free-tongued [plethodontid] salamanders" (Dunn 1926, p. 27). Dunn noted the double premaxillae, lack of sexual dimorphism, and "ancestral" ecological relationships. Noble (1931) believed *Gyrinophilus* and *Pseudotriton* to be the most primitive plethodontids, but noted that in several features the former was more derived than *Eurycea*. According to Platt (1935) *Gyrinophilus* is the most primitive of the eastern free-tongued plethodontids, with *Stereochilus*, *Typhlomolge*, and *Typhlotriton* being "degenerate, specialized forms" arising from a *Gyrinophilus*-like ancestor, which also gave rise to *Pseudotriton* and *Eurycea*. Wake (1966, p. 63) believed *Gyrinophilus*, *Stereochilus*, and *Pseudotriton* to be "the most primitive generic group in the family [Plethodontidae]."

It is true that *Gyrinophilus* and its allies are in some respects primitive. However, I believe that certain so-called primitive features are in fact derived. There can be little question that structurally *Plethodon* is distinctly more primitive than any living euryciine. I argue below that *Eurycea* is probably as primitive as *Gyrinophilus* and that the reproductive patterns of the Euryciini and Desmognathini may be of secondary origin. *Plethodon* is representative of the ancestral plethodontid, at least structurally.

REMARKS. This species has a long, relatively narrow body with a short, robust tail. The trunk is more or less cylindrical and well muscled. There are between 16 and 19 costal grooves, with counts of 17 and 18 being the most common (see Brandon 1966). Limbs are quite small for a normally metamorphosing salamander of its body size, but they are not diminutive.

Epaxial musculature (see Fig. 65).- The *dorsalis trunci* is similar to that of *Desmognathus*. In dorsal view the medial parts of the anterior flexures are hidden by the musculature of the opposite side. Thus the paired myomeres of either side meet in a forwardly pointing V. This differs from *D. fuscus*, in which the anterior flexures are almost completely exposed in dorsal view. When the myomeres are displaced laterally the anterior flexures are seen to be developed in a manner similar to *D. fuscus*. Each anterior flexure is relatively short, extending to about the midpoint of the neural arch of the first vertebra of the pair that its myomere spans. There is a slight overlap of these flexures.

The main bodies of the myomeres are thick, extending posterodorsally from between adjacent vertebrae and ribs. The muscle fibers align anteroventrally, there being no superficial layer of anteroposterior fibers as is seen in *Desmognathus*. From the posteromedial edge of each main body a large deep posterior flexure extends posteromedially and ventrally. This is hidden beneath the anterior flexure of the next posterior myomere, and inserts on the lateral edge of the neural arch of the following vertebra. These deep posterior flexures are presumably homologous to the posterior septa encountered in ambystomatids, being produced by means of invasion of muscle fibers so that stronger direct pull is produced on the vertebrae. Whereas ambystomatids and hynobiids have the septa only in the posterior half of the column, *Gyrinophilus* and other plethodontids tend to have deep posterior flexures throughout the column. Owing to the presence of these flexures, each myomere is excavated anteriorly so as to accommodate the posterior flexure of the next anterior myomere and to produce its own posterior flexure.

Hypaxial musculature (see Fig. 65).- The *subvertebralis* of this species differs from that of *Desmognathus*, but is of basically similar plan. Although closely comparable to *Desmognathus*, it is derivable from the condition of *Eurycea*. The main part of each myomere, beneath and also distal to the ribs, is composed of ventral fibers extending anterolaterally to underlap the anterior neighbour. The myomeres extend a significant distance distal to the ribs. The intercostal fibers run posterolaterally, eventually forming the *o. e. profundus* distally and ventrally.

Posterior basapophyseal muscles are present along the column, although posterior basapophyses are lacking. Whether these should be termed posterior flexures rather than basapophyseal muscles is problematical, but they are closely comparable to the basapophyseal muscles of *Pseudotriton* and *Desmognathus*. Each vertebra gives rise to a pair of septa, one from either side of the posterior cotyle. These parallel the centrum of the next posterior vertebra and provide attachment for muscle fibers. These fibers fan posteriorly to the centrum, paralleling septum, and posterior flexure of the following vertebra. The posterior flexures, along with the internal basapophyseal septa, form cone-in-cone structures along the column, as is seen in *Pseudotriton* and *Desmognathus*.

The spinal nerves exit as in other plethodontids, passing posterolaterally through the *subvertebralis* until just before the latter's distal edge. The nerves are here exposed to the peritoneal cavity for a very short distance, and then extend between the *transversus* and *o. e. profundus*.

Lateral abdominal musculature (see Fig. 65).- The lateral abdominal musculature is almost identical to that of *D. fuscus*. Laterally the *o. e. superficialis* bridges the epaxial myomeres and the *rectus abdominus*, both of which it overlaps slightly. In contrast to *D. fuscus*, the fibers of the *o. e. superficialis* extend posteroventrally at an angle slightly displaced from the vertical. A *rectus lateralis* is present. The *o. e. profundus* lies deep to the *o. e. superficialis* and is a direct ventral continuation of the *subvertebralis*. The fibers of this layer extend posteroventrally at an angle slightly displaced from the horizontal.

The *transversus* is applied against the inner surface of the *o. e. profundus*. It is relatively thick, its fibers running anteroventrally, and not divided by myocommata. A few muscle fibers from the *transversus* attach to the anterodistal edge of each rib. Ventrally there is a slight overlap onto the *r. a. superficialis*, to which it is bound by tough fascia. The *rectus abdominis* is divided into two portions, as in all other plethodontids here described. The *r. a. superficialis* overlaps the *o. e. profundus* externally, as described for other species above. The *r. a. profundus* is a long band extending between the hyoid apparatus and the pelvic girdle. It may be separated into two layers: an external one with fibers extending anteromedially, and an internal unit with fibers running anterolaterally. The *r. a. profundus* is an integral part of the hyobranchial apparatus anteriorly. The main portion sweeps anteriorly dorsal to the lateral projection of the *os thyroideum*, while a small slip inserts posteromedially on this bone. The main part continues anteriorly to attach to the ventral surface of the second ceratobranchial medially, to the posterolateral surface of the first basibranchial, and to the ventral surface of the first ceratobranchial medially. The posterior origin of the *r. a. profundus* is on the ventral surface of the ischio-pubic cartilage and the anterior half of the ischium. This is as in hynobiids and other plethodontids.

The larval *rectus abdominis* is simple, formed of a single unit of muscle fibers extending anteroposteriorly. It is continuous with both the *o. e. profundus* and the *o. internus* dorsally. The larvae thus differ from the adults in the presence of an *o. internus* and only a simple *rectus abdominis.*

Pseudotriton ruber (Latreille 1802)

RANGE. Found from New York state, southward to western Florida, and then westward along the Gulf Coast to western Mississippi. From here the western limits extend north through Mississippi, along the western border of Tennessee and through Kentucky and southern Ohio to include most of Pennsylvania (Bishop 1943).

HABITAT. "Found in and about clear, cold springs and small streams of wooded ravines, swamps, open fields, and meadows. The adults are often terrestrial during the summer . . . hiding beneath logs, bark, and stones" (Bishop 1943, p. 389). The larval period is long, lasting at least two years, with adult size almost reached prior to metamorphosis (Dunn 1926). The eggs are guarded (Salthe and Mecham 1974).

FOSSIL RECORD. This species is reported from the Pleistocene of Georgia by Holman (1967).

RELATIONSHIPS. Dunn (1926) believed *Pseudotriton* to be close to *Gyrinophilus*, but less primitive. Noble (1931) and Platt (1935) suggested that it was involved in the ancestry of *Eurycea*. As noted by Wake (1966), only *Gyrinophilus* and *Pseudotriton* lack sexual dimorphism among the more terrestrial Euryciini, while these two genera, plus *Stereochilus* and *Typhlotriton*, are the only plethodontids retaining the presumably primitive condition of vomerine teeth continuous with the palatal tooth patches. Study of the trunk musculature shows these taxa to be closely related, but I do not consider it profitable to construct detailed generic phylogenies within the Euryciini.

REMARKS. The genus *Pseudotriton* is long-bodied and proportioned as its relative *Gyrinophilus*, but the trunk is somewhat more muscular and robust. The limbs are very short, but powerful. The tail is short and but slightly compressed laterally. The usual number of costal grooves is 16, but counts of 15 and 17 are also common (Bishop 1943, Dunn 1926). The vertebrae are small and delicate for the size of the animal and are deeply buried by the trunk musculature. The shape and proportions of the trunk vertebrae recall *Desmognathus*, although *Pseudotriton* lacks the various projections of the former (see Fig. 16). The trunk musculature definitely indicates the validity of separate generic status for *Pseudotriton*, as argued by Wake (1966) on other criteria.

Epaxial musculature (see Fig. 66).- The general form of the epaxial myomeres is in some respects more similar to *Desmognathus* than to that of *Gyrinophilus*. The neural arch is correspondingly similar to that of *Desmognathus*, having a low neural crest (lacking in *Gyrinophilus*) and a similarly formed hyperapophysis. Pterygapophyses, subcentral keels, and ventral lamellae are, however, lacking in *Pseudotriton*. The anterior flexures are short and relatively narrow, extending only about one quarter of the distance over the neural arch of the anterior vertebra of the pair spanned by its myomere. There is very slight overlap of the anterior flexures. Almost the full extent of each flexure is evident in dorsal view, contrasting to the condition in *Gyrinophilus*.

The main body of each myomere is massive, extending laterally beyond the distal ends of the ribs. Each myomere rises steeply from between adjacent ribs. Unlike in *Desmognathus*, there is no superficial layer of muscle fibers extending anteroposteriorly over the main bodies of the myomeres. The muscle fibers extend anterolaterally throughout the main bodies, extending down almost to the level of the ribs. Deep posterior flexures are large, running posteromedially and slightly ventrally to insert just in front of the hyperapophysis of the following vertebra. Each myomere thus affects three vertebrae directly. In their points of insertion, the deep posterior flexures of the *dorsalis trunci* resemble those of *Desmognathus* more than those of *Gyrinophilus*.

Deep to the myomeres, and obscured by the anterior flexures and deep posterior flexures, are found the hyperapophyseal muscles. These are each provided with a long, thin septum and are developed as in other plethodontids.

Hypaxial musculature (see Fig. 66).- A thin median band beneath the centra and the intercentral joints are exposed to the peritoneal cavity. Well-developed posterior basapophyses are present in the anterior region of the trunk.

As in *Gyrinophilus*, there is an obtuse anterior flexure in each myomere, the apex being beneath the distal end of the ventral rib-bearer. Medially each myomere has a broad, long, and deep posterior flexure extending backwards. This flexure is underlapped by muscle fibers of the following myomere. In the medial portion, muscle fibers extend anteroposteriorly, whereas more laterally beneath the ribs the superficial fibers proceed anteriolaterally. The main body of each myomere extends distal to the ends of the ribs for a distance about equal to the lengths of the ribs. The main portion of the myomere inclines posteroventrally in the first three or four myomeres of the trunk. In the remainder of the column they incline anteroventrally. This deflection of the myomeres is similar to *Gyrinophilis*, whereas in *Desmognathus* they descend more or less straight ventrally. The intercostal muscles are posterolaterally oriented, blending with the *o. e. profundus* laterally and ventrally.

The posterior flexures form a series of cone-in-cone structures along the column. Muscle fibers radiate from each flexure to the internal septum of its posterior neighbour. Dorsal to each posterior flexure, and partially continuous with it, is a wide, relatively short septum attaching to each posterior basapophysis. Muscle fibers extend posteriorly, posterolaterally, posterodorsally, and posteromedially from this septum, forming the posterior basapophyseal muscle. The distinction of basapophyseal muscles is somewhat arbitrary, owing to the fact that they partially merge with the posterior flexures ventrally.

The spinal nerves have the typical plethodontid exits from the column and then extend laterally and slightly posteriorly through the *subvertebralis*. They reach the peritoneal surface of the myomeres just distal to the ends of the ribs and run over this surface for a short distance until they disappear external to the *transversus*. Between the *o. e. profundus* and *transversus*, each nerve is attached to a myocomma. Ventrally, the spinal nerves pass between the *transversus* and the *r. a. profundus* to disappear within the *r. a. superficialis*.

Lateral abdominal musculature (see Fig. 66).- The *o. e. superficialis* is located externally along the lateral body wall. This layer is divided by transverse myocommata and is composed of muscle fibers extending posteroventrally at an angle slightly offset from the vertical. The *o. e. superficialis* is thick and very wide, extending between the *dorsalis trunci* and *rectus abdominis*, both of which it overlaps. The width of this layer contrasts with its narrowness in *Gyrinophilus* and *Desmognathus*.

A *rectus lateralis* is located deep to the *o. e. superficialis* and ventral to the *dorsalis trunci*. The *o. e. profundus* is a very thick layer, segmented by myocommata, and a direct continuation of the *subvertebralis*. Its fibers run posteroventrally at an angle little displaced from the horizontal. Ventrally it blends with the *r. a. superficialis*, except for a slight overlapping by the latter.

The *transversus* is the next layer, there being no trace of the *o. internus*. It is relatively thick and extends between the *subvertebralis* dorsally and the *r. a. superficialis* ventrally. Its muscle fibers extend anteroventrally. As in hynobiids and the more primitive ambystomatids, the *transversus* of *Pseudotriton* is divided by myocommata in its dorsal third, but ventrally it is not segmented. The *rectus abdominis* is composed of two units and does not differ significantly from that of *Gyrinophilus*.

The various resemblances of *Pseudotriton* to *Desmognathus* are perhaps to be interpreted as owing to convergence or parallelism. The habitat and life style of *Pseudotriton* are somewhat similar to those of certain species of *Desmognathus*, although the burrowing adaptations of the skull and associated musculature of the latter are absent. I suggest, however, that the resemblances are more significant than this. In many ways *Pseudotriton* is structurally ancestral to the desmognathines. If the Desmognathini are indeed the derived sister-group of the Euryciini (i.e. they share a common ancestor) as argued below, the resemblances are to be interpreted as owing to parallelism in closely related lineages.

Tribe Desmognathini nov.

Desmognathus fuscus (Rafinesque 1820)

RANGE. Found from the St. John's River, New Brunswick, southward to central Florida, across the Gulf Coastal Plain to western Texas and then northward to southeastern Oklahoma. The northern limits run through Arkansas, northern Mississippi, eastern Tennessee, Kentucky, and Illinois, and then through Indiana and Ohio to Lake Erie (Bishop 1943, Conant 1958).

HABITAT. The larval period is relatively short and is spent in streams, although the eggs are laid on land and hatchlings live for 15 or 16 days on land before entering the water (Noble 1931). Adults are found along "the margins of streams and springs, leaf-filled trickles, springy banks where the soil is constantly moist, and often [in] the beds of partially dry streams in deep ravines" (Bishop 1943, p. 188). They are powerful burrowers found under logs, rocks and other debris, and are primarily, but not exclusively, terrestrial.

FOSSIL RECORD. Vertebrae referable to *Desmognathus* species are known from the uppermost Pleistocene of Virginia (Guilday 1962).

RELATIONSHIPS. *Desmognathus* has been traditionally considered to be a relatively primitive, although divergently specialized, plethodontid, with ecological relationships and life history similar to the ancestral stock (Dunn 1917, 1926, Wake 1966). *D. fuscus* can be grouped with other members of the genus in the following series: *D. quadramaculatus*, *D. monticola*, *D. fuscus*, *D. ochrophaeus*, and *D. wrighti*. This series (see Dunn 1917, 1926, Organ 1961) shows a trend from completely aquatic larvae and highly aquatic adults (*D. quadramaculatus*) to completely terrestrial larvae and adults (*D. wrighti*).

I argue below that this sequence does not necessarily document the development of a higher degree of terrestrialism within the Desmognathini, but is perhaps a secondary reversion to aquatic larvae. This hypothesis is not necessarily preferable to the traditional one, as it too results in certain inconsistencies (see Conclusions). I also suggest, less tentatively, that the Desmognathini are not as isolated as previously thought, but that they are structurally derivable from the Euryciini, with which they share a close sister-group relationship.

REMARKS. The trunk is long and robust, the limbs small but active in locomotion, and the tail is short and thick, of large diameter behind the cloaca and tapering rapidly to a point. There are usually 14 costal grooves and the trunk is extremely well muscled for a terrestrial, non-paedogenic salamander. There is also a high degree of differentiation within the *dorsalis trunci*. *D. fuscus* is capable of moving large rocks as it burrows beneath them. Rapid locomotion over land is snake-like, the limbs held out of the way against the body.

In addition to *D. fuscus*, specimens of *D. monticola* (aquatic larvae, adults inhabiting stream banks) and *D. ochropaeus* (very short aquatic larval period, adults found in forest litter away from streams, postmetamorphic individuals in stream banks) were available. These were all but identical to *D. fuscus* in terms of the trunk musculature.

Epaxial musculature (see Fig. 67).- The *dorsalis trunci* is a large mass dorsal and, especially, lateral to the vertebral column. Anterior flexures are short and relatively narrow. A thin superficial layer of muscle fibers extends anteroposteriorly over the *dorsalis trunci*. Beneath this layer, in the main bodies of the myomeres, the fibers run anteroventrally between myosepta. In the anterior flexures the deeper fibers fan forward from each apex. The main body of each myomere rises steeply posteriorly from between adjacent ribs. From the posteromedial corner of each myomere a large deep posterior flexure tapers backwards. This extension inserts on the hyperapophyseal area of the following vertebra and does not differ from the same flexure in other plethodontids.

Pterygapophyses are developed on the more anterior trunk vertebrae, extending posterolaterally from the dorsal surfaces of the posterior zygapophyses (see Fig. 16). These provide areas of insertion for discrete blocks of muscles originating on the dorsolateral edges of the neural arch of the following vertebra. These muscles parallel the hyperapophyseal muscles laterally, and are here termed pterygapophyseal muscles. They presumably function to augment the hyperapophyseal muscles, providing two distinct points of insertion on each half of the vertebra.

This confirms Wake's (1966, p. 41) suggestion that the pterygapophyses of desmognathines provide "additional attachment sites for dorsal spinal muscles." However, his suggestion that these muscles would help "raise the skulls of the three genera to open their mouths," is unlikely. The mass of musculature inserting on the posterior of each vertebra is not increased by the differentiation of the pterygapophyseal muscles. Rather, it is re-arranged. Also, these muscles do not pull so as to depress the posterior of the vertebra to which they insert (which would thereby raise the anterior of the body), but serve to swing the vertebrae from side to side on the pivot provided by the opisthocoelous intercentral joint. Finally, the pterygapophyses extend posterolaterally, shifting the point at which the pull is concentrated away from the midline. This would not be efficient if the function of these muscles was to raise the head. It is a logical construction to meet demands for lateral movement. Therefore, these muscles perhaps serve to increase fine control for lateral movement of the head and anterior part of the body in feeding. Presumably they also assist in burrowing, by moving the head and forelimbs from side to side to force a path through the substrate and to move rocks out of the way.

A small but distinct hyperapophyseal muscle is found medial to each pterygapophyseal muscle. This muscle is developed as in other plethodontids, originating over the lateral half of the neural arch of one vertebra and inserting on one of the hyperapophyseal "horns" of the next anterior vertebra by means of a septum.

Hypaxial musculature (see Fig. 67).- The *subvertebralis* is readily derivable from the condition in *Pseudotriton* or *Gyrinophilus*. Posterior basapophyses are present throughout the trunk, but are usually lacking on the first presacral vertebra. On the more anterior vertebrae (T1 through T9 or T10) a ventral projection is found just posterior to the anterior condyle (see Fig. 16). This serves as an area of attachment for muscle fibers in the anterior parts of the column where it is more strongly developed. Muscle fibers associated with these projections extend anterolaterally in the more forward parts of the trunk and straight anteriorly further back. The ventral projection probably also serves to brace the intercentral joint, as it projects forward between the posterior basapophyses of the next anterior vertebra. This interlocking is especially developed between the centra of the atlas and second cervical and is associated with the areas in which the posterior basapophyses and pterygapophyses are most developed.

Each posterior basapophysis gives rise to a large posterior basapophyseal muscle, which inserts onto a long, thin septum attaching to the posterior basapophysis. From this septum muscle fibers fan posteriorly. Each basapophyseal muscle is surrounded ventrally by a myoseptum that separates it from the associated myomere. These covering myosepta are underlain by muscle fibers so that a cone-in-cone structure results. Lateral to these, the main bodies of the myomeres are very thick. In the more anterior myomeres the ventral muscle fibers extend anterolaterally. More posteriorly they come to align anteroposteriorly. Dorsal to this thick ventral unit, the intercostal fibers tend to be aligned strictly anteroposteriorly.

Spinal nerves exhibit the basic plethodontid pattern.

Lateral abdominal musculature (see Fig. 67).- In comparison to other non-paedogenic urodeles, the lateral abdominal musculature of *D. fuscus* is very thick. However, it retains the typical structure of other adult plethodontids, lacks the *o. internus*, and is not foetalized. The relatively thick *o. e. superficialis* is segmented by myocommata and slightly overlaps the *dorsalis trunci* and *rectus abdominis*. The fibers of this unit extend dorsoventrally with no posteroventral deflection.

The *o. e. profundus* is thick and the fibers extend posteroventrally. Dorsally a few fibers attach to the distal edge of each rib, and ventrally the *o. e. profundus* blends with the *r. a. superficialis*, although it is partially overlapped by a part of the latter. The internal *transversus* is very thick, its fibers running anteroventrally at an angle slightly displaced from the vertical. Dorsally, some of the muscle fibers attach to the ends of each rib, acting in a manner antagonistic to the fibers of the *o. e. profundus*. The *transversus* is not divided by myocommata and overlaps the *r. a. superficialis* ventrally.

Just ventral to the *dorsalis trunci* and between the two layers of the external oblique is a narrow *rectus lateralis*. As in the other plethodontids dissected, the *rectus abdominis* is divided into two distinct units.

Leurognathus marmoratus Moore 1899

RANGE. This monotypic genus "inhabits trout streams in the southern Appalachian Mountains from southwestern Virginia to northeastern Georgia" (Martof 1962, p. 1).

HABITAT. Almost strictly aquatic, it inhabits "the bottoms of cold, oxygen-rich streams. Areas with rough, broken rocks and loose gravel are preferred to those with water-worn (rounded) rocks and tightly packed sand . . . the largest populations [therefore] occur in the medium and smaller sized streams. . . . The vast majority of specimens are found in . . . [shallow] waters. Rapids and riffles are more densely occupied than are pools or areas wherein the flow is less rapid and deeper. *Leurognathus* is strongly rheocolous" (Martof 1962, p. 7). Eggs are laid in water, and "the female stays with her eggs throughout the entire [2½ month] period of development" (Martof 1962, p. 18).

FOSSIL RECORD. None known.

RELATIONSHIPS. Moore (1899) recognized the close alliance of *Leurognathus* and *Desmognathus*. The structural and ecological resemblances of the two genera are well documented (Dunn 1917, 1926, Hairston 1949, Organ 1961), with *Leurognathus* interpreted as divergently specialized away from the supposed trend towards increased terrestrialism seen within *Desmognathus*. It is undoubtedly true that *Leurognathus* is derived, but there remains the possibility that the fully aquatic habits (and correlated structures) represent the culmination of the trend seen in *Desmognathus*, rather than a divergence from the main line. There are several sorts of evidence in support of this contention, which interprets aquatic reproduction in *Desmognathus* as a secondary phenomenon (see Conclusions).

REMARKS. *Leurognathus* is extremely similar to *Desmognathus quadramaculatus*, a slightly more terrestrial species, in terms of external features. It is distinguishable by means of relatively minor proportional differences, of which the slit-like internal nares are perhaps the most diagnostic (Martof 1963). *Leurognathus* is a relatively large, heavy-bodied salamander with robust limbs. The tail is distinctly compressed and not notably elongate. The skull is flattened, as in *Desmognathus*, but more pointed. Costal grooves vary in number, being either 13 or 14 (Bishop 1943).

Leurognathus occupies one end of the aquatic-terrestrial cline in the Desmognathini. There are, however, two features seemingly in conflict with its aquatic existence:

1) retention of the nasolabial groove, supposedly a terrestrial adaptation, and
2) retention of a large, posteriorly free tongue pad. The pad is relatively larger than that of *Desmognathus fuscus*, which is more terrestrial.

The only reasonable explanation for the retention of a "land" tongue with a well-developed pad and long epibranchials would seem to lie in the periodic drying of the streams inhabited by *Leurognathus*. At such times, although on an irregular basis, it would be forced into a terrestrial existence (Martof 1962). As noted by Darwin (1859) periodic times of stress impose very pronounced selection, Martof (1962) suggested that this periodic drying could account for the retention of the nasolabial groove. A second part of the answer is probably historical. Derived from terrestrial ancestors (see Conclusions), *Leurognathus* was equipped with these structures and was able to maintain them in order to survive periods of aridity.

Except for Eaton (1956), no one has questioned recognition of *Leurognathus* as distinct from *Desmognathus*. Martof (1962, p. 34) justified separation on the basis of "morphological distinctiveness and differences in basic adaptive trends." Nevertheless, *Leurognathus* differs structurally from *Desmognathus* in only minor details. *L. marmoratus* can be distinguished from the species of *Desmognathus*, but this in itself does not support generic status. The differences are largely proportional and/or matched in one or another species of the latter genus. Cranial structure, trunk musculature, hyobranchial apparatus, and their morphoclines within the Plethodontidae demonstrate the derived nature of *Leurognathus*, and its structural continuity with *Desmognathus*. This leaves the criterion of "basic adaptive trends" in support of generic separation, but only if the trend in *Desmognathus* is truly towards increasing terrestrialism. It is, perhaps, equally probable that the aquatic eggs and larvae of *Desmognathus* are owing to secondary reversion (see Conclusions). If so, continued recognition of *Leurognathus* cannot be supported.

Epaxial musculature (see Fig. 68).- The structure of the *dorsalis trunci* is all but identical to that of *D. fuscus*. The myomeres have a thin external layer of muscle fibers extending anteroposteriorly. Beneath this, in the main bodies of the myomeres, fibers extend anterolateroventrally. *Leurognathus* differs from *D. fuscus* in the virtual absence of pterygapophyses from the column, these structures occurring only in the pectoral region (see also Wake 1966). Correlated with this is the lack of pterygapophyseal muscles from the trunk region posterior to the pectoral girdle. Hyperapophyseal muscle blocks appear to be dorsally confluent with the ventral parts of the anterior flexures.

Hypaxial musculature (see Fig. 68).- The *subvertebralis* differs to a somewhat greater degree from that of *D. fuscus* than does the *dorsalis trunci*. In both species the basic structure is the same, with the posterior basapophyseal muscles covered by a layer of myoseptal tissue, but in *Leurognathus* the covering is not underlain by anteroposterior muscle fibers to any degree. *Leurognathus* also shows the development of a small forwardly projecting septum from the front of each myomere at the latter's anterior apex. This septum sends fibers anteromedially to the paralleling posterior basapophyseal muscle and anterior to the next myoseptum.

Laterally the main bodies of the myomeres are as in *D. fuscus*, except for a slight anterior inclination. The spinal nerves are developed as in *Desmognathus*, but are exposed to the peritoneum for a short distance dorsal to the *transversus* prior to continuing ventrally between the latter and the *o. e. profundus*.

Lateral abdominal musculature (see Fig. 68).- All layers and their basic relationships are as in *D. fuscus*. The *o. e. superficialis* extends somewhat less dorsally in *Leurognathus*, not overlapping the *dorsalis trunci*. The fibers, however, extend dorsoventrally and are connected to a tough dorsal and ventral fascia, which passes over the *dorsalis trunci* and *rectus abdominis*, as in *D. fuscus*. The *o. e. profundus* is the same in the two taxa. The *transversus* is distinctive in two respects. Its dorsal attachments reach further medially along the anterior faces of the ribs than is the case in *D. fuscus*. The *transversus* is invaded by myocommata at the dorsal edge, at which points the spinal nerves extend external to it. In other features, the lateral abdominal musculature is as in *D. fuscus*.

vii) Family Salamandridae Gray 1825

a) Subfamily Salamandrinae Tschudi 1838

Salamandra salamandra (Linnaeus 1758)

RANGE. This species is widespread throughout much of Europe, except the British Isles and Scandinavia. It barely extends into the USSR, and there are populations in the Middle East and northwest Africa (Thorn 1968, Steward 1969).

HABITAT. "The main requirements . . . are shade and moisture. Throughout most of its range, it has a predilection for wooded areas, particularly in hilly country. The nature of the soil and vegetation is of great importance, this species preferring deciduous woods with leaf litter, such as beech forests, and . . . avoiding coniferous forests on dry soils" (Steward 1969, pp. 49-50). Moderate elevations are preferred and the animals are generally nocturnal or crepuscular, being about in the day only when there are heavy rains. They are terrestrial, the females only entering water when they deposit the larvae, which are born alive. The larvae are of the typical pond type with broad tail fins, prominent limbs, and large gills (see Steward 1969). In the other species of the genus, *S. atra*, the young are born alive as terrestrial miniatures of the adult.

FOSSIL RECORD. The genus has an extensive time range. Estes et al. (1967) tentatively referred trunk vertebrae, caudal vertebrae, and humeri to *Salamandra* species from Paleocene deposits in France. From the published figures, the specimens appear to show resemblances to *Pleurodeles* also. *Salamandra* is known additionally from the Oligocene, Miocene and Pleistocene of Europe, with the following named species:

S. broilii Schlosser 1922 (middle Oligocene to middle Miocene, Germany); *S. sansaniensis* Lartet 1839 (wide distribution in the Oligocene and Miocene of Europe, see Estes and Hoffstetter 1976); *S. goussardiana* Lartet 1839 (Miocene, France); *S. laticeps* von Meyer 1960 (Miocene, Czechoslovakia, referred to *Tylototriton* by Noble [1928], but this revision was rejected by Herre [1935b]); *S. mimula* Brunner 1957, *S. perversa* Brunner 1957, and *S. pottensteinia* Brunner 1956 (Pleistocene, central Europe). It is probable that certain of these taxa could be synonymized.

In addition to these species, there have been various fossil genera named that are either synonymous with *Salamandra* or closely allied. *Praesalamandra* Brunner 1957 and *Palaeosalamandra* Herre 1949, from the German Pleistocene and middle Miocene respectively, are all but certainly *Salamandra*. *Megalotriton* Zittel 1888, from the Oligocene and Miocene of Europe, is also very close to *Salamandra*. Herre (1949) considered that it participated in a structural series as follows: *Megalotriton* - *Salamandra broilii* - *Salamandra salamandra*. *Voigtiella* Herre 1949, from the Miocene of Germany, was placed in a separate subfamily in the Salamandridae by Brame (1967). However, the figured vertebra (Herre 1949, fig. 4) shows resemblances to *Salamandra* in some respects, and in his original descriptions Herre (1949) explicitly claimed it to be a highly developed member of the *Salamandra* group. *Dehmiella* Herre and Lunau (1950), from what can be gained from the descriptions and figured material, also seems to show affinities to *Salamandra*. Estes (1970) states that it is an "immature" *Salamandra*.

It is probable that at least some of these genera should be synonymized with *Salamandra*. Pending much needed work, it can be said that the genus *Salamandra* and its relatives are at least as old as the Paleocene.

RELATIONSHIPS. Bolkay (1928) considered *Salamandra* to be a primitive salamandrid, deriving it from an *Ambystoma*-like ancestor. He recognized *Salamandra* and *Chioglossa* to be closely related and distinct from the other salamandrids. By contrast, Dunn (1922) and Noble (1931) believed the newts to be more primitive, citing the frontosquamosal arch, high neural spines, long ribs, and long maxillae as primitive characters. Noble (1931) stated that *Salamandra* was derived in lacking the *obliquus internus* and in having a divided *rectus abdominis*.

It is evident that the characters presumed to be primitive for the Salamandridae by Dunn and Noble are, in fact, highly derived. This follows from ex-group comparisons, study of larval characters, morphocline polarities, and the criterion of parsimony (see Conclusions). Studies of the trunk musculature necessitate re-interpretation of Noble's (1931) conclusions as to the nature of the lateral abdominal musculature of *Salamandra*. The more primitive adult salamanders lack the *o. internus* and have a double *rectus abdominis* (compare hynobiids, ambystomatids, and plethodontids), whereas larval urodeles have a simple *rectus abdominis* and an *o. internus*. In this regard, as in many others, *Salamandra* is more primitive than the newts, as interpreted by Bolkay (1928), Herre (1935b), and von Wahlert (1953).

Wake and Özeti (1969) claimed that *Tylototriton* and *Pleurodeles* are the most primitive salamandrids, with *Salamandra* being a more derived offshoot. As is argued below, this interpretation cannot be accepted. The evidence from the trunk musculature and from the cranium indicate conclusively that *Salamandra* is the most primitive living salamandrid, although *Tylototriton* and its allies are closely related. The similarity of various of the early Tertiary fossils to both *Salamandra* and *Pleurodeles* may document this relationship.

Wake and Özeti (1969) also grouped *Salamandrina* with *Salamandra* and *Chioglossa*. Resemblance of *Salamandrina* to the other two genera is, nevertheless, exceedingly slight and owing only to convergence of the hyobranchial apparatus. As noted by Noble (1931, p. 475) and others, *Salamandra* "is merely a European newt lacking the fifth toe." It is most closely related to *Pleurodeles* and *Tylototriton* (see below).

More specifically, Estes and Hoffstetter (1976, p. 297) note that *Salamandra sansaniensis* "was widely distributed in Europe during the Oligocene and Miocene; its area of distribution was fragmented by Pleistocene glaciations, and its abundant populations seem to have given rise to the living *S. salamandra* and *S. atra*.

REMARKS. *S. salamandra* has a stout, robust body with 10 or 11 costal grooves. The limbs are relatively powerful and the tail short and cylindrical. It has a relatively greater mass of trunk musculature than the newts (subfamily Pleurodelinae) and a weakly developed opisthocoely. Young postmetamorphic individuals retain a fully amphicoelous condition. In addition to adult *S. salamandra terrestris*, very small individuals of *S. atra* were dissected, and found to have trunk musculature identical to that of the other species. Both species have a double row of poison glands running middorsally along the back and tail (see Fig. 70). These glands are sunk into the *dorsalis trunci*, causing alteration of the anterior flexures.

Epaxial musculature (see Figs. 69 and 70).- The *dorsalis trunci* differs significantly from that of salamanders of other families, but it is also different from that of the newts (although *Pleurodeles* shows some resemblance), notably as regards the greater development of the anterior flexures. Middorsally the paired poison glands are recessed into the epaxial musculature, causing a unique displacement of the myomeres, which are depressed along parallel lines between the apices of the anterior flexures. The tips of the plate-like, slightly bifurcate hyperapophyses are not covered by musculature owing to the presence of these glands. The displacement of the myomeres is not figured.

The anterior flexures do not meet along the median, but are shifted laterally to expose the paired hyperapophyseal muscles medially. The septum supporting each of these latter muscles appears as a posterior continuation of the medial septum of the next forward anterior flexure. In contrast to the situation in plethodontids, the septa of the hyperapophyseal muscles are oriented vertically. Anterior flexures are markedly elongate, broad, and shallow, extending far forward over their anterior serial homologues. At the apices short septa project forward into the musculature of the next flexure. The situation of the anterior flexures and hyperapophyseal muscles is not likely primitive for the Salamandridae, but owing to modification because of the poison glands.

The main bodies of the myomeres are small, rising relatively steeply from between the ribs. Each myomere extends laterally only to the end of the bony portions of the ribs. The cartilaginous tips of the ribs proceed lateroventrally beneath the *o. e. superficialis* into the *rectus lateralis*. *Salamandra* also differs from the families described above in lacking deep posterior flexures throughout the column.

Hypaxial musculature (see Fig. 69).- The *subvertebralis* is basically similar to that found in the Plethodontidae. In superficial ventral view the myomeres appear as simple blocks, each extending between two vertebrae. When the thin ventral layer of fibers is removed, the plethodontid-like posterior flexures are evident. A septum extends posteromedially from each ventral rib-bearer to the lateral border of the posterior cotyle of the same vertebra. This forms the posterior wall of the posterior flexure. From the rear border of each flexure an elongate, broad septum extends back to the level of the transverse process of the following vertebra. This septum gives rise to muscle fibers that fan posteriorly into the next posterior flexure. Estes et al. (1967) note the presence of small (undoubtedly posterior) basapophyses on some skeletons of *Salamandra*. In view of the positional relationships and uniqueness of the posterior flexure, it is all but certain that this system is phylogenetically homologous to that of the plethodontids, representing a shared-derived character.

The ventral surfaces of the centra are not underlain by muscle fibers, this area being occupied by adipose tissue. Next to the centra the ventralmost muscle fibers align anteroposteriorly. Moving laterally, the fibers come progressively to extend anterolaterally. Eventually these fibers form the *transversus*, with no discernible break between it and the *subvertebralis*. The phylogenetic origins of this seemingly unique system are uncertain. Dorsal to the thin ventral layer the intercostal muscles extend anteroposteriorly. This group proceeds laterally slightly beyond and below the ends of the ribs to form the *rectus lateralis*.

The spinal nerves exit intravertebrally throughout the column, extending laterally and somewhat posteriorly through the *subvertebralis* to an area just distal to the transverse processes. From here the nerves are applied against the ventral surface of the *subvertebralis*. The nerves extend ventrally along the peritoneal surface of the *transversus*, along the lines of the myocommata. About midway along the *transversus*, each nerve extends through the latter unit to run between it and the *obliquus externus*.

Lateral abdominal musculature (see Fig. 69).- The musculature of the lateral and ventral body walls differs significantly from that of plethodontids, but resembles that of hynobiids in some respects. The body wall is relatively thin and very simple in its gross anatomy. Externally, a wide *obliquus externus* extends between the pelvic and pectoral girdles. This band is divided vertically by myocommata, which are ventral continuations of the septa forming the epaxial and subvertebral myomeres. The *o. externus* overlaps the *dorsalis trunci* above and the *rectus abdominis* below. The muscle fibers extend posteroventrally. Dorsally, in the anterior portion of each segment, several muscle fibers are loosely attached to the external surface of the cartilaginous tip of a rib. The *obliquus externus* of *Salamandra* is probably homologous to the *o. e. superficialis* of other urodeles, the *o. e. profundus* being absent.

Deep to the *o. e. superficialis*, just below the epaxial musculature, is a thin *rectus lateralis*. This is composed of fibers extending anteroposteriorly between the cartilaginous tips of the ribs and is a direct continuation of the *subvertebralis*. It extends ventral to the ribs for a short distance, and in this area is perhaps the remains of the *o. e. profundus*. As in plethodontids, the more primitive ambystomatids, and most hynobiids, the *o. internus* is absent, the *transversus* being directly applied against the *o. e. superficialis*. The *transversus* is segmented in its dorsal half, the remainder being undivided. The fibers extend anteroventrally, extending just over the boundary between the two portions of the *rectus abdominis*. Dorsally the *transversus* is continuous with the *subvertebralis*.

The *rectus abdominis* is indistinctly divided into two parts. Both of these are thin and composed of fibers running anteroposteriorly between adjacent myocommata. The more medial *r. a. superficialis* forms the ventral musculature of the belly. It is not covered by any other layers of musculature, except laterally where it is slightly overlapped by the ventral edges of the *o. e. superficialis* (externally) and the *transversus* (internally). The *r. a. profundus* is somewhat thicker than the other part of the *rectus abdominis*. It is located between the *transversus* and the *o. e. superficialis*, and lateral to the *r. a. superficialis*. It differs markedly from that of plethodontids and some Pleurodelini in being a simple layer firmly attached to the *r. a.*

superficialis. According to Böttcher (1883), *Chioglossa* Bocage 1864 has a free *r. a. profundus*. *Tylototriton* and *Salamandrina* (see below), as well as some hynobiids and plethodontids, also have this free portion of the *rectus abdominis*. It is likely, therefore, that the condition in *Salamandra* is secondary.

b) Subfamily Pleurodelinae nov.

Tribe Pleurodelini Bonaparte 1838

Pleurodeles waltli Michahelles 1830

RANGE. Found "throughout the southern and western parts of the Iberian Peninsula," and also in northwestern Morocco (Steward 1969, p. 80). A second species, *Pleurodeles poireti* (Gervais 1835), is found scattered along the Mediterranean coast of Tunisia and Algeria (Thorn 1968).

HABITAT. Although fully capable of coming onto land, this species is almost completely aquatic, being found in ponds, swamps, and other sorts of standing water. Estivation in the mud of temporarily dry ponds is common. It is relatively sluggish, moving along the bottom amongst plentiful aquatic vegetation to capture food. Moving prey, including large invertebrates and the larvae of other amphibians, is taken (Thorn 1968, Steward 1969).

FOSSIL RECORD. No fossil material has been assigned to *Pleurodeles*, but Herre (1941) named and described *Palaeopleurodeles hauffi* from the upper Miocene of Germany, which may prove to be a member of the extant genus. Other *Pleurodeles*-like fossils are discussed under *Tylototriton*.

RELATIONSHIPS. Bolkay (1928) derived *Pleurodeles* from a common ancestor shared with the other newts, placing it closest to *Salamandrina* and *Triturus*. He considered it to be derived with respect to *Salamandra* and *Chioglossa*. Noble (1931) believed *Pleurodeles* to have descended from a *Tylototriton*-like ancestor and to be otherwise most closely related to *Triturus* and *Euproctus*.

Herre (1935b) thought this genus to have been derived from a common ancestor shared with *Tylototriton* and *Salamandrina*. These three genera were believed to be closely related to *Salamandra* and *Chioglossa*. Thorn (1968) agreed, but indicated that *Pleurodeles* was most closely related to *Tylototriton*. On the basis of courtship data, Salthe (1967) informally grouped *Pleurodeles* with *Tylototriton*, *Salamandra*, and *Chioglossa*, all of which have the male capturing the female from below. Wake and Özeti (1969) claimed *Pleurodeles* was a primitive salamandrid, derived from the basal stock just after the divergence of *Tylototriton* and prior to the split of *Salamandra*, *Chioglossa*, and *Salamandrina*.

My studies are in close agreement with Herre (1935b) and partially controvert the phylogenetic theory of Wake and Özeti (1969). *Pleurodeles*, *Tylototriton*, and *Salamandrina* are to be classified in a subfamily Pleurodelinae, along with the other newts, and a tribe Pleurodelini, contrasted to the tribe Triturini. The Pleurodelini include the most primitive newts, which are derived with respect to *Salamandra* and *Chioglossa*.

REMARKS. These are very large newts, growing to as much as 16 inches total length. The trunk is robust, with 13 or 14 myomeres between the pelvic and pectoral girdles. The limbs are powerful and large, especially the forelimbs, which have an important function in breeding (see Thorn 1968, Salthe 1967). There is extensive calcification of the ypsiloid process, ischio-pubic cartilage, and supra-scapular and procoracoid cartilages. The skull is flat and wide, especially posteriorly. Well-developed frontosquamosal arches are present, although one specimen available to me has a ligamentous arch on the right side. A large muscle extends between the external surface of the scapula and the rear of the cranium in a dorsolateral direction. This presumably relates to the presence of the body arch and is found in most other newts. The posterior dentigerous projections of the vomers are short and widely separated posteriorly. The nasals are separated by the double premaxillae.

Epaxial musculature (see Fig. 71).- The *dorsalis trunci* is thick and extends laterally almost to the tips of the ribs. Excepting the most posterior three or four pairs of ribs, which are covered by the epaxial myomeres, the ribs are sharply pointed at their tips. These lie free between the trunk musculature and the skin. When handled roughly, the points pierce the skin, functioning to discourage predation (Steward 1969).

The myomeres incline posteriorly at a steep angle. Anterior flexures are broad and rounded anteriorly. A long, tough septum extends forward from the apex of each flexure and muscle fibers fan forward from this, forming the body of the next anterior flexure. The anterior flexures are very similar to those of *Salamandra*, but are shorter and do not expose the hyperapophyseal muscles. The flexures meet medially to cover the neural crests and aliform processes. Each aliform process gives rise to a pair of hyperapophyseal muscles, which are developed as in the newts described below. The septa are more or less horizontal and muscle fibers extend posteriorly from them to originate on the sides of the neural crests and roofs of the neural arches. In the main bodies of the myomeres the muscle fibers extend anteriorly and slightly ventrally.

Hypaxial musculature (see Fig. 71).- The *subvertebralis* is composed of two ill-defined layers. The more ventral layer has fibers that extend posterolaterally between the ribs and is continuous with the *o. e. profundus* laterally and ventrally. The more dorsal intercostal fibers extend anteroposteriorly and are continuous with the *rectus lateralis*. Medially, between the transverse processes of adjacent vertebrae, the fibers of the two units blend together, proceeding anteroposteriorly. The *subvertebralis* does not extend right up to the centra, but leaves a small area next to each intercentral joint that is filled with connective tissue and adipose tissue. As in other newts, the *transversus* extends ventral to the *subvertebralis* to insert on the ventrolateral edges of the centra.

Spinal nerves exit intravertebrally and extend laterally ventral to the *subvertebralis*. At the level of the distal ends of the transverse processes the nerves pass through the *transversus* to lie against the peritoneum. This position is retained to well beyond the tips of the ribs.

Lateral abdominal musculature (see Fig. 71).- The lateral abdominal musculature is thick, but composed of only three layers. The *o. e. superficialis* differs from that of most other newts in that it does not originate on the ribs, but along each myoseptum just below the ribs, thus freeing the latter for their anti-predator function. The fibers of the *o. e. superficialis* extend posteroventrally to slightly overlap the *rectus abdominis*. There are no segmenting myocommata in this unit.

The *rectus lateralis* is not associated with the ribs, but its fibers extend anteroposteriorly between adjacent myosepta. It blends ventrally with the more superficial fibers of the *o. e. profundus*. The fibers of the latter extend posteroventrally at a lesser angle than those of the *o. e. superficialis*. Ventrally the *o. e. profundus* is overlapped externally by a flap from the simple *rectus abdominis*, the muscle fibers of which run anteroposteriorly. The fibers of the *rectus abdominis* and *o. e. profundus* merge imperceptibly.

As in other newts, the *transversus* originates along the lateral edges of the centra. There are few gaps in the intercentral areas and those that are present are very narrow. This is presumably an aquatic adaptation (see description of neotenic *Notophthalmus*), as more terrestrial newts tend to have intercentral gaps in the *transversus*. The fibers of this unit proceed anterolaterally beneath the *subvertebralis* and then anteroventrally to insert along the *rectus abdominis*.

Tylototriton andersoni Boulenger 1892

RANGE. This species is found on the Ryukyu Islands (Okinawa, Amami, and Tokuno) south of Japan. The other five recognized species are from restricted areas on the mainland of China and into Tibet and southeast Asia (Thorn 1968).

HABITAT. Neither the species nor the genus are well known ecologically. *T. andersoni* is terrestrial, being found in the humid, shaded areas of dense vegetation in mountain forests. *T. chiuhaiensis* is terrestrial during the cold season and aquatic during the warm. *T. verrucosus* is found in shaded, humid areas under rocks and plant debris, although Anderson (1871) collected adults in flooded rice fields. The remaining species are said to be terrestrial (see Liu 1950, Thorn 1968), but little else is known. Breeding behavior in *T. verrucosus* occurs in water as in *Pleurodeles* and the pond-type larvae develop in still water (Thorn 1968).

FOSSIL RECORD. The genus is recognized from the Eocene and Miocene of Europe: *T. primigenius* Noble 1928 (upper Miocene, Switzerland); *T. koswigi* Herre 1949 (Miocene, Germany); and *T. weigelti* Herre 1935b (middle Eocene, Germany). Noble (1928) suggested that *Salamandra laticeps* von Meyer 1960, from the Miocene of Czechoslovakia, was a young *Tylototriton*. Although Brame (1967) lists without comment this species as *Tylototriton laticeps*, Herre (1935b, 1950) explicitly rejected Noble's suggestion and considered it a member of the genus *Salamandra*.

According to Herre (1935a,b), *Polysemia ogygia* (Goldfuss) from the Miocene of Germany is closely related to *Tylototriton*, as is the lower Miocene *Heliarchon furcillatus* von Meyer from Czechoslovakia. Kuhn (1962) considered the latter species to be also related to *Chelotriton* Pomel. Herre (1949) suggested the following structural series as reflective of phylogeny: *Pleurodeles* and *Palaeopleurodeles* - *Grippiella* Herre - *Tischleriella* Herre - *Chelotriton* and *Tylototriton*. He noted the close resemblance of *Chelotriton* to *Tylototriton* and claimed that *Grippiella* and *Tischleriella* were intermediate between the living *Tylototriton* and *Pleurodeles*.

As the fossil genera *Polysemia*, *Heliarchon*, *Grippiella*, *Tischleriella*, and *Chelotriton* all show varying degress of similarity to *Tylototriton*, there is certainly the need for synonymizing many of these names. Study of these taxa is urgently needed and would provide valuable phylogenetic information. Estes and Hoffstetter (1976) have described additional material of *Chelotriton paradoxus* Pomel 1853 from the Miocene of France and note that the name *Chelotriton* has priority over *Tylototriton*.

RELATIONSHIPS. *Tylototriton* is most closely related to *Pleurodeles* and *Salamandrina* (see discussion under *Pleurodeles*).

REMARKS. Salamanders of the genus *Tylototriton* are large, robust newts with wide, flattened skulls. *T. andersoni* (the alligator newt) and *T. verrucosus* are heavily built with well-developed costal tubercles and broad, flat heads. By contrast, *T. taliangensis* and *T. kweichowensis* are more *Pleurodeles*-like, with less widened skulls, costal tubercles and middorsal crests weakly developed, and long, laterally compressed, and high tails (see Liu 1950, Thorn 1968). These features probably reflect a more aquatic way of life in the latter two species.

T. andersoni, of which only a single poorly preserved specimen was available, is remarkable for the development of tuberosities in the skin and spines extending from many of the bones. From the postero-lateral corner of each quadrate a small, sharp spine curves abruptly to extend anteriorly. This spine is covered by a thick tubercle of skin.

The cranium is robust, markedly flattened, and greatly widened posteriorly, being spade-shaped in dorsal view. The quadrates are produced anteriorly to articulate with the posteriorly elongate *pars facialis* of each maxilla. The *pars palatina* of the maxilla is very wide and, posteriorly, extends medially to meet the pterygoid.

The frontosquamosal arch is well developed, its dorsal surface extensively sculptured with pits and ridges. A distinct middorsal crest extends posteriorly from the skull, down the trunk and along the tail. This is formed by the dorsally extended neural crests of the vertebrae, which are each provided with a narrow, pitted dorsal plate. The trunk vertebrae between the girdles bear ribs that have sharp distal tips. In addition, an auxiliary spine is present more medially on these ribs. The ends of the ribs and the auxiliary spines are free of muscle fibers, but lie beneath raised and thickened tuberosities of skin. Although the tubercles are very tough, it may be that the spines puncture the skin when the newt is grasped by a predator, as in *Pleurodeles*.

There is marked differentiation of the ribs along the column. Those behind the atlas are modified in association with the scapulocoracoids and associated musculature. Those of the midtrunk are elongate, whereas the presacral ribs are much shortened, producing a distinct "lumbar" region. The trunk is dorsoventrally flattened and wide. Owing to the poor preservation of the available specimen, no attempt has been made to figure the musculature and descriptions are tentative.

Epaxial musculature.- In so far as it can be interpreted, the *dorsalis trunci* is extremely similar to that of *Salamandrina*. It differs primarily in that the dorsal surfaces of the ribs are largely free of muscle fibers. As noted by Riese (1891), the vertebrae of *Salamandrina* are very like those of *Tylototriton*, a similarity reflected in the structure of the *dorsalis trunci*.

Hypaxial musculature.- The *subvertebralis* also resembles that of *Salamandrina*, being composed of only a single unit of muscle fibers in each intervertebral segment. The fibers extend anteroposteriorly between adjacent transverse processes and posterolaterally between the ribs. *Tylototriton* lacks robust ventral lamellae and muscle fibers do not underlie the ribs (contrast *Salamandrina*). Spinal nerves exit intravertebrally and proceed laterally and ventrally as in *Salamandrina*.

Lateral abdominal musculature.- *Tylototriton* has only the *obliquus externus* and *transversus* forming the lateral body wall, and neither of these is divided by myocommata (compare *Salamandra*). The *transversus* is formed as in *Salamandrina*, but the *obliquus externus* differs in lacking the confluence with the intercostal musculature dorsally. As in *Salamandrina* there is a free *r. a. profundus*. This is somewhat unexpected, in that *Tylototriton* supposedly has a "water-tongue" (see Wake and Özeti 1969). This would seem to provide this newt with two mutually exclusive structures. However, the available information indicates that *Tylototriton* is quite terrestrial and it may well be that the tongue is considerably freer and more protrusable than has been recognized.

In total, the structure of the cranium, of the vertebral column, and of the trunk musculature provide convincing evidence of very close relationship between *Tylototriton* and *Salamandrina*. Any similarities between the hyobranchial apparatus of *Salamandrina* and the salamandrines (and these are relatively slight) are owing to convergence. This is in agreement with the findings of earlier workers (Bolkay 1928, Herre 1935c) and necessitates rejection of part of the phylogenetic hypothesis of Wake and Özeti (1969).

Salamandrina terdigitata (Lacépède 1788)

RANGE. This monotypic genus has a limited distribution, being "confined to the mountain slopes along the west side of the Apennines [in Italy]" (Steward 1969, p. 83).

HABITAT. This is a terrestrial newt, found in "wooded areas, where it lives in the damp leaf litter under the trees, and normally remains near small [clear] streams" (Steward 1969, p. 83). Mating occurs on land, the female then laying eggs in small clusters attached to stones or plant debris in slow-moving streams. The lungs are extremely reduced, and the tongue (modified from the newt-type) is adapted for protrusion from the mouth (see Thorn 1968, Steward 1969).

FOSSIL RECORD. There is no record for this genus, but *Palaeosalamandrina dehmi* Herre 1949, from the Miocene of Germany, is known from vertebrae that are very like those of *Salamandrina*. It is likely that this species should properly be classified as *Salamandrina dehmi*.

RELATIONSHIPS. Bolkay (1928) thought this genus to be related to the newts (i.e., salamandrids exclusive of *Salamandra* and *Chioglossa*). Herre (1935b) believed *Salamandrina*, *Pleurodeles*, and *Tylototriton* to be derived from a common ancestor. In contrast to all previous workers, Wake and Özeti (1969) allied *Salamandrina* with the salamandrines. As shown elsewhere, this interpretation is not supported by the available evidence. As Thorn (1968) indicated, *Salamandrina* is related to *Pleurodeles* and *Tylototriton*. These three genera, which I classify together in the Pleurodelini, form a group that is derived with respect to *Salamandra* and *Chioglossa*.

REMARKS. These are small, relatively robust newts with long tails. The sacrum is T14, although the ribs of the first presacral and first caudosacral vertebrae are closely associated with it. The ribs of the midtrunk region are long and heavy, tapering distally to a point. There is some differentiation of the ribs in the trunk. They are short in the area of the limb girdles and progressively lengthen from either end towards the middle of the trunk (see Wiedersheim 1875 for excellent figures and description). The cranium has a fully developed bony frontosquamosal arch and is otherwise also of the newt pattern. The orbits are greatly enlarged. As in *Tylototriton* and *Pleurodeles*, the premaxillary bones are paired. The tongue is protrusible, the adults feeding on small insects.

Epaxial musculature (see Fig. 72).- The *dorsalis trunci* bears little resemblance to that of *Salamandra*, but is very like that of *Tylototriton*. The myomeres are not raised above the level of the ribs, and barely cover them. Thus, the posterior inclination of the myomeres seen in most other salamanders is lost. The dorsal plate on the neural crest of each vertebra is above the level of the *dorsalis trunci* and the neural crests are little raised above the neural arches.

The superficial layer of the *dorsalis trunci* is formed of fibers extending anteroposteriorly. Anterior flexures are greatly reduced in comparison to other newts, although similar to those of *Tylototriton*, and each is provided with a short, anteriorly directed septum. These septa receive muscle fibers from the hyperapophyseal septa of the aliform processes. The myomeres of the epaxial complex extend to the distal tips of the ribs.

Next to the neural crests and beneath the superficial fibers are located the hyperapophyseal muscles. These are developed as in other newts. Each consists of a septum extending posteriorly from one edge of the aliform process in the vertical plane. Fibers extend posteriorly between this septum and the neural crest of the next posterior vertebra. In other newts the fibers in this area tend to proceed posteromedially. From the lateral surface of each septum fibers extend posterolaterally to the forward septum from the anterior flexure.

Hypaxial musculature (see Fig. 72).- As in other pleurodelines, the *subvertebralis* is underlain by the *transversus*. The hypaxial myomeres are very thin. Muscle fibers run posterolaterally between the ventral lamellae, which are not underlain by fibers of the *subvertebralis*. Between adjacent ribs fibers extend posterolaterally. The ribs are only underlain by subvertebral fibers for their distal halves. The intercostal fibers have only a single orientation.

The spinal nerves exit intravertebrally, extending through the *subvertebralis* and then the *transversus* to the peritoneal surface at the level of the ends of the rib-bearers. The nerves proceed along the peritoneum to beyond the ends of the ribs, at which point they are external to the *transversus*.

Lateral abdominal musculature (see Fig. 72).- The lateral abdominal musculature is simplified in comparison to that of most other newts, but is essentially similar to that of *Tylototriton* and *Triturus helveticus*. The *transversus* extends medially to insert along the lateral edges of the centra. In the anterior part of the column it arises along the entire lengths of the centra, as well as intercentrally. In the posterior half of the column there are small intercentral gaps in the *transversus*. Myocommata are absent. The *transversus* underlaps the *r. a. superficialis* ventromedially.

Only a single layer of the *obliquus externus* is present and this is not divided by myocommata. Its fibers extend posteroventrally to overlap the *r. a. superficialis*. Dorsally the *o. externus* is continuous with the intercostal musculature, probably indicating its homology with the *o. e. profundus* of other salamanders. There is no trace of a *rectus lateralis* or *o. internus*.

The *rectus abdominis* is composed of two units as in *Tylototriton*, the more primitive hynobiids and ambystomatids, and most plethodontids. The *r. a. superficialis* is a simple band of anteroposteriorly directed muscle fibers, which are separated by myocommata. Dorsolaterally each half of the *r. a. superficialis* is inserted between the ventral edges of the *o. externus* and *transversus*. It slightly overlaps the *r. a. profundus*, which is covered internally by the *transversus* and externally by the *o. externus*. The *r. a. profundus* is relatively narrow, segmented by myocommata, and composed of muscle fibers that are slightly twisted. It originates on the pelvic girdle and extends anteriorly to insert onto the hyobranchial apparatus. It is free within the lateral abdominal musculature and functions as the retractor of the tongue during feeding. The *r. a. profundus* is thus developed as in the Plethodontidae (q.v.) and performs the same functions in both groups.

Tribe Triturini nov.

Notophthalmus viridescens (Rafinesque 1820)

RANGE. "The species is found in . . . the Maritime Provinces and southern Quebec and . . . Ontario, and the eastern United States west to Minnesota, eastern Iowa, extreme eastern Kansas, eastern Oklahoma, and south-central Texas" (Mecham 1967, p. 53.1).

HABITAT. The larvae and usually the mature adults are aquatic, found in "ponds and pools . . . with abundant submerged vegetation, and in swamps and quiet pools of small streams" (Mecham 1967, p. 53.1). After metamorphosis, the animal goes through a completely terrestrial red eft stage, returning to water several years later when sexually mature. Also, however, adults are sometimes found in terrestrial situations and neoteny is common (see Gage 1891, Noble 1926, 1929, Healy 1974, 1975).

FOSSIL RECORD. In addition to a Pleistocene record from Florida (Holman 1962) of *Notophthalmus viridescens*, three exclusively fossil species of the genus are recognized. *N. slaughteri* comes from the Miocene of Texas (Holman 1966), *N. robustus* is known from the Miocene of Florida (Estes 1963), and *N. crassus* comes from the Miocene of South Dakota (Tihen 1974).

RELATIONSHIPS. Bolkay (1928) united the North American newts in one genus, *Diemictylus*, believing them to be related to the Asian newts.

Noble (1931) considered *Notophthalmus* to be most closely related to the European *Triturus*, but that *Taricha* originated from an Asiatic species. Herre (1935b) also thought *Notophthalmus* to be derived from *Triturus*, suggesting that the fossil salamander *Oligosemia* represented a stock ancestral to the North American genus. He considered *Taricha* to be more primitive, having given rise to the *Triturus* complex of genera. Steiner (1950) postulated separate origins for the North American genera, in a manner similar to that of Noble (1931), suggesting that *Taricha* was most closely related to *Pleurodeles* and entered North America via Asia, whereas *Notophthalmus* originated from *Triturus*. Wake and Özeti (1969) would derive the North American genera from a common ancestor that is in turn related to *Triturus*.

The trunk musculature of *Notophthalmus* is somewhat similar to that of *Triturus vulgaris* and *T. cristatus*, but even more like that of the Asian *Cynops* and *Paramesotriton*. There is also resemblance to these latter genera in the presence of high neural crests with laterally expanded dorsal plates. *Taricha* bears no special resemblance in the trunk musculature to the Asian newts or *Notophthalmus*. Nevertheless, in some respects the Miocene *Taricha miocenica* is intermediate between the two genera of North American newts (Tihen 1974) and the courtship patterns of the two are the same (Salthe 1967). The exact relationships of the two North American genera to each other as well as to other salamandrids are uncertain. There is little question that they belong in the Triturini, and there is some evidence of close relationship between the two (courtship behavior seems especially important, see Salthe 1967). I include the two in the *Notophthalmus* generic group, considered to be closest to the *Cynops* group (see Conclusions).

REMARKS. Of the four named subspecies of *N. viridescens* the following were available for study: *N. viridescens viridescens*, *N. viridescens dorsalis*, and *N. viridescens louisianiensis*. *Notophthalmus perstriatis* was also studied, but not found to differ from *N. viridescens*. The majority of the observations come from specimens of *N. v. louisianiensis* from Florida. These were of interest because both neotenic and metamorphosed adults were available. The trunk musculature was found to differ significantly between neotenic and transformed members of this subspecies, but not amongst the metamorphosed adults of the available species and subspecies.

N. viridescens is a small, but robust newt. In males the hindlimbs are large and powerful, in correlation with breeding behavior. The tail is long and narrow, and especially high in breeding males. The trunk is short in comparison to other North American salamanders and costal grooves are not evident. Very young larvae have amphicoelous vertebrae, whereas older larvae and adults are fully opisthocoelous. In neotenic individuals the trunk is thick, with an expanded *dorsalis trunci* and heavy lateral abdominal musculature. In the latter, the anterior condyles of the centra appear less strongly calcified, being tipped with a distinct cartilaginous cap. In two gravid neotenic females the vomers retain an essentially larval aspect, whereas the pterygoids are more or less as those of metamorphosed individuals. In neotenic males from the same areas the vomers are of normal adult form and the hyobranchium is non-larval.

Epaxial musculature (see Figs. 73 and 74).- The *dorsalis trunci* differs between neotenic and metamorphosed individuals. In the latter, a robust, plate-like expansion is present on top of each neural crest and not covered by musculature. The *dorsalis trunci* is developed as in certain species of *Triturus*, notably *T. vulgaris*. Each myomere is applied against the dorsolateral surface of the vertebrae and ribs, sloping ventrally from the neural crests to the distal portions of the ribs. The myomeres are inclined very slightly posteriorly. Anterior flexures are very small, extending a short distance beyond the aliform process of the anterior vertebra of the pair spanned by the myomere. Muscle fibers in the main bodies of the myomeres run anteroposteriorly. Hyperapophyseal muscles are of typical newt pattern, originating on the lateral surface of a neural crest and dorsal surface of the neural arch of one vertebra and inserting on the aliform process of the next anterior vertebra, both by muscle fibers and a vertical septum.

In neotenic individuals the neural crests lack the capping plate and are buried by musculature. The anterior flexures are much larger than in non-neotenic specimens, extending forward over the posterior third of the neural crest of the first vertebra of the pair spanned by the myomere. The form of the anterior flexure is somewhat similar to that of *Dicamptodon*, almost certainly owing to convergence. The main bodies of the myomeres are inclined posteriorly to a greater degree than in metamorphosed individuals. Hyperapophyseal muscles are developed as in non-neotenes. In the structure of the *dorsalis trunci* and amount of musculature, neotenic *Notophthalmus* resemble *Siren*.

Hypaxial musculature (see Figs. 73 and 74).- The *subvertebralis* is almost identical in neotenic and non-neotenic specimens. It is underlain by the *transversus*, which attaches to the ventrolateral edges of the centra. As in other newts, there are no subvertebral flexures, each myomere being restricted to a single intervertebral area. The ventral-most layer of muscle fibers extends anteroposteriorly under the ventral lamellae. The myosepta extend up under these lamellae, along the area of the ventral rib-bearers. In this feature *Notophthalmus* differs from *Triturus*, which has the fibers running only between the ventral lamellae. There is a distinct tendency for neotenes to lack some of the posterior portions of the ventral lamellae. In these cases, most vertebrae retain fully developed lamellae, but some lack the rear of the lamellae on one side or the other.

Laterally, beyond the ends of the transverse processes, the fibers of the ventral layer come to align anterolaterally, eventually blending with the *obliquus internus* distal to the ribs. Above the ventral layer, fibers run anteroposteriorly between the anterior and posterior edges of adjacent ventral lamellae. Laterally this unit becomes the intercostal musculature and extends posterolaterally. It finally blends with the *o. e. profundus*. Although somewhat different from other newts, the condition of the *subvertebralis* is readily derivable from that of an ancestor having ventral lamellae on the transverse processes (e.g., *Triturus vulgaris*).

The spinal nerves have intravertebral exits, extending posterolaterally through the *subvertebralis* to the peritoneal surface. Here they extend a short distance on the internal surface of the *transversus* before proceeding ventrally, one spinal nerve per myocomma, between the *transversus* and *o. internus*.

Lateral abdominal musculature (see Figs. 73 and 74).- The lateral abdominal musculature of metamorphosed *N. viridescens* is like that of *Triturus vulgaris*. The *transversus* originates along the anterior three-quarters of each centrum. From here the fibers extend antero-laterally and ventrally along the inner surfaces of the *subvertebralis*, *o. internus*, and to the start of the *rectus abdominis* ventrally and medially. At each intercentral joint there is a gap in the *transversus*, presumably to prevent bulging of the unit during lateral flexure of the column.

In neotenes there are no gaps in the *transversus*, which originates along the entire length of the column without interruption. Ventrolaterally each centrum develops a long, low flange to which the *transversus* attaches. Some non-neotenic individuals have small flanges on the centra, but these are not developed to the same degree. Very large adults, of which only metamorphosed individuals were available, have thick, low subcentral keels on the centra. The ventrolateral flanges are especially well developed on the more anterior trunk vertebrae. In both neotenic and metamorphosed specimens the external (dorsal) surface of the *transversus* is joined to the myosepta of the *subvertebralis*. These attachments are lacking in the area of the *o. internus*. Neotenes seem to have the *transversus* more tightly attached to the myosepta.

The remaining parts of the lateral abdominal musculature are similar in neotenes and metamorphosed specimens, except for the greater mass laterally and very thin *rectus abdominis* in the former. In large individuals of *N. v. viridescens*, the *o. e. superficialis* originates at points over the distal tips of the ribs. However, in neotenic and non-neotenic *N. v. louisianiensis* (unfortunately smaller than the specimens of the other subspecies) the *o. e. superficialis* is applied over the surface of the *rectus lateralis* and *o. e. profundus*, instead of directly onto the ribs. From the dorsal origins, the muscle fibers extend posteroventrally to overlap the *rectus abdominus*. The *o. e. superficialis* is not segmented.

A narrow *rectus lateralis* extends anteroposteriorly between the ends of the ribs. This unit appears somewhat better developed in the non-neotenes. The *o. e. profundus* and *o. internus* are both present and segmented by myocommata. They are similar to the same units in *Triturus vulgaris*, but in *Notophthalmus* the *o. e. profundus* is a direct continuation of the *subvertebralis*. The fibers of the two units align at approximately right angles to one another. Ventromedially they change orientation and blend together, forming the *rectus abdominis*. In internal view the latter is not distinct from the *o. internus*, but it overlaps the *o. e. profundus* externally. This overlap is especially well developed in neotenes, extending dorsally between the *o. e. superficialis* and *o. e. profundus*.

Taricha torosa (Rathke *in* Eschscholtz 1833)

RANGE. Found in the coastal regions of California from Baja California to almost the Washington border. One subspecies is isolated in the interior of California (Stebbins 1954).

HABITAT. "In and near streams in canyons of the coastal mountains . . . [coinciding] with distribution of the coast and interior live oaks and . . . into the Digger and yellow pine zones" (Stebbins 1954, p. 48). Breeding occurs in streams, lakes, and ponds. Adults, especially the males, spend much time in water even outside of the breeding season.

FOSSIL RECORD. None of the living species of *Taricha* are known as fossils. *Taricha oligocenica* is known from the upper Oligocene of Oregon (van Frank 1955) and *T. miocenica* from the lower Miocene of Montana (Tihen 1974). Tihen (1974) assigned these to a subgenus *Palaeotaricha*, distinguishing them from the living species (subgenus *Taricha*). They differ from the extant species in having well-developed dermal caps on the neural crests, a condition similar to *Notophthalmus* (see Fig. 19, also Tihen 1974, fig. 1). A new species of *Taricha*, from the Oligocene John Day Formation of Oregon, is referable to the subgenus *Taricha* and is currently being described (Naylor, in prep.).

RELATIONSHIPS. On the basis of vertebral resemblances between *Palaeotaricha* and *Notophthalmus*, Tihen (1974) postulated a sister-group relationship between the two genera of North American salamandrids. This seems reasonable at present and I place *Taricha* with *Notophthalmus* in the *Notophthalmus* group within the tribe Triturini (see discussion under *Notophthalmus*).

REMARKS. These are large newts, having a relatively long trunk and large, robust limbs. The tail is very long and narrow. There are usually nine myomeres between the limb girdles and the trunk is relatively heavy and somewhat compressed dorsoventrally. The skull is low and wide, resembling that of some of the Asian newts. The trunk musculature of *T. torosa* and *T. granulosa* is all but identical in gross anatomy.

Özeti and Wake (1969) describe and figure only a single pair of radii in the hyobranchium of *Taricha*. According to Cope (1889) and Smith (1927), however, there are two pairs of radii in this genus, as in *Salamandra*, *Pleurodeles*, and *Tylototriton*. My dissections confirm the observations of Cope and Smith: *Taricha* has two pairs of radii on the first basibranchial.

Epaxial musculature (see Fig. 75).- The *dorsalis trunci* is a thin band of muscle, extending longitudinally on either side of the neural crests. It extends laterally to the distal ends of the ribs, at which point it blends into the *rectus lateralis*. There is no horizontal septum segregating the epaxial musculature from the lateral abdominal. The myomeres are inclined very slightly posteriorly, and medially they extend forward into small, but distinct anterior flexures.

Anterior flexures abut medially on thin, low neural crests, which lack dorsal plates. The neural crests may or may not be covered by musculature. Each anterior flexure sends forward a thin, deep septum, from which muscle fibers fan into the body of the next anterior flexure. In some specimens the anterior septa join to an aliform process anteriorly, completely covering the associated hyperapophyseal muscle laterally. Muscle fibers from the hyperapophyseal septa extend posterolaterally to attach to the septa of the anterior flexures. The hyperapophyses are of typical newt pattern. Muscle fibers in the main body of each myomere extend in a primarily anterolateral direction. The ends of the ribs are covered by epaxial musculature.

Hypaxial musculature (see Fig. 75).- As in other newts, the *transversus* must be removed to expose the *subvertebralis* in ventral view. The latter is composed of only a single unit of fibers, thereby differing from *Notophthalmus*. Muscle fibers originate on the anterior surface of each transverse process and extend anterolaterally to insert on the posterior, distal edge of the next anterior transverse process. Adipose tissue fills the gap between each transverse process and the lateral wall of the centrum. Ventral lamellae are lacking, there being only a thin, narrow strut of bone joining the posteromedial part of each transverse process to the centrum.

Distal to the transverse processes, between the ribs, intercostal fibers extend posterolaterally. There is a very sudden change between the fibers running between transverse processes (anterolateral alignment) and those joining the ribs. Beyond the ends of the ribs the *subvertebralis* is continuous with the *o. e. profundus*.

Spinal nerves are essentially as described in *Notophthalmus*.

Lateral abdominal musculature (see Fig. 75).- The *o. e. superficialis* is developed in a manner similar to that of *Notophthalmus*. There are no segmenting myocommata, and the fibers extend posteroventrally. The unit originates over the areas of the ribs, but without direct attachment. The *rectus lateralis*, located deep to the above, is a ventral continuation of the epaxial musculature. It is segmented by myocommata and continues ventrally to blend with the *o. e. profundus*.

The latter unit is very thin, being composed of a single layer of fibers proceeding posteroventrally between segmenting myocommata. It blends with the *rectus abdominis* ventrally, but the latter also overlaps the *o. e. profundus* externally. There is no *o. internus*. The *transversus* is quite thick, originating along the lateral edges of the centra and from the ventral surfaces of the transverse processes medially. A long, narrow gap is left at the level of each intercentral joint. The fibers of the *transversus* extend anterolaterally and anteroventrally, eventually overlapping the *rectus abdominis* slightly. There are no myocommata in the *transversus*.

The *rectus abdominis* is approximately twice as thick as the musculature of the lateral wall of the body. There is no division into a superficial and a deep portion, but it is more complex than that of *Notophthalmus*. A thin fold of the *rectus abdominis* overlaps the *o. e. profundus* externally. Internally, the *rectus abdominis* is folded against the inner surface of the *o. e. profundus*, where it is separated into two lateral bands. The more medial is composed of fibers extending anteroposteriorly. Lateral to this, a group of muscle fibers extends anteromedially between the myocommata and external to this are the fibers of the *o. e. profundus*. This situation vaguely resembles the differentiated *rectus abdominis* of *Tylototriton* and *Salamandra*, perhaps an indication that *Taricha* is the most primitive living member of the Triturini.

Cynops pyrrhogaster (Boie 1826)

RANGE. This species is found on the Japanese islands of Hondo, Shikoku, Kyushu, and Yaku (Thorn 1968).

HABITAT. "Widely distributed and common, inhabiting streams, ponds, reservoirs, and roadside drains, but probably confined to the lower altitudes" (Stejneger 1907, p. 19). The adults are largely aquatic in clear water (Thorn 1968). In the laboratory, feeding occurs readily in or out of the water.

FOSSIL RECORD. Young (1965) described *Procynops miocenicus* from the upper Miocene of Shantung, China. No other fossil material of *Cynops* or *Cynops*-like species is known. Three nearly complete skeletons of *Procynops* are known. These have "very feeble" limbs, are smaller than adults of any living species of *Cynops*, and may well be larvae.

RELATIONSHIPS. On the basis of cranial osteology, Bolkay (1928) believed *Cynops* (including *Paramesotriton chinensis*) to be related to *Taricha*, *Notophthalmus*, *Tylototriton*, and *Pachytriton*. Chang (1935) placed *Cynops orientalis* in a new genus *Pingia* and classified the monotypic *Hypselotriton* as *Cynops wolterstorffia*. He considered *Cynops* to be closely related to "*Trituroides*" (now *Paramesotriton chinensis*). Chang's nomenclatorial changes have not been followed by subsequent workers.

Herre (1935b) classified the species of *Cynops* then recognized in *Triturus*, but in the same year he and Wolterstorff (Wolterstorff and Herre 1935) recognized *Cynops* as a valid genus. Wake and Özeti (1969) believed *Cynops* to be closest to *Hypselotriton* and *Pachytriton*, and probably to *Paramesotriton*, as well. According to Thorn (1968), *Cynops* and *Paramesotriton* are related to the species of *Triturus* that Bolkay (1928) included in "*Palaeotriton*" (type species: *T. vulgaris*). This species group of *Triturus* does show resemblances to the Asian newts, but the meaning of these similarities is not certain. For convenience the Asian newts are here united into the *Cynops* group, including *Cynops*, *Paramesotriton*, *Hypselotriton*, and *Pachytriton*.

REMARKS. *Cynops pyrrhogaster* is a medium-sized to small newt with a thick trunk, almost square in cross-section. The tail is markedly laterally compressed, elongate, and high. The limbs are not enlarged, but they are robust. A strong frontosquamosal arch is present and the skull is heavy and elevated, similar to that of *Notophthalmus*. The sacrum is usually T14. In one specimen the first caudosacral vertebra retains a pair of short, robust ribs, and is involved in supporting the pelvic girdle. A line of protuberant glands extends down each side of the trunk, along the line at which the epaxial musculature and the *rectus lateralis* meet. Large paratoid glands are also present. These newts are difficult to skin, the trunk musculature adhering to the very thick and tough skin.

Epaxial musculature (see Fig. 76).- The dorsal surfaces of the neural crests are laterally expanded, forming robust, dorsally pitted, and elongate triangles in dorsal view. These are not covered by epaxial musculature and form a bony ridge down the back, presumably having a defensive function. The vertebral column and epaxial musculature are differentiated along the trunk. Two regions may be distinguished: an anterior "thoracic" region extending from T1 to approximately T10, and a posterior "lumbar" region comprising the immediately presacral vertebrae (T10 or 11 to T13). No difference between the vertebrae of each area is evident, but the ribs differ markedly. In the "thoracic" region the ribs are long and ventrally curved, extending well beyond the limits of the *dorsalis trunci*. This is especially true just behind the pectoral girdle. From this point posteriorly the ribs gradually decrease in length. In the "lumbar" region they are very short and completely enclosed within the *dorsalis trunci*. Although there is a gradual decrease in length through the "thoracic" series, there is a more abrupt transition to the "lumbar" region.

The *dorsalis trunci* is developed as in *Taricha torosa*. Anterior flexures are small, but well developed, and large hyperapophyseal muscles are present.

Hypaxial musculature (see Fig. 76).- The *subvertebralis* is covered ventrally by the *transversus*, as in other newts. It is composed of three units, similar to the condition of *Triturus vittatus*. Ventrally and laterally a part of the *obliquus internus* extends under the *subvertebralis* proper. The fibers of this single, thin layer proceed anterolaterally. Medially muscle fibers run anteroposteriorly between the ventral lamellae of adjacent vertebrae. Lateral to this the fibers extend posterolaterally and are located above those of the medial extension of the *o. internus*. When the fibers of these ventral portions are removed, the third unit is evident. Its fibers originate on the anterior edge of one ventral lamella and proceed anteriorly and anterolaterally to insert on the posterior border of the transverse process of the next anterior vertebra. Ventrally and laterally this unit blends with the fibers of the more ventral unit to form the *o. e. profundus*.

The spinal nerves exit intravertebrally and extend ventrally in the same manner as in the newts described above.

Lateral abdominal musculature (see Fig. 76).- The *o. e. superficialis* is found on the external surface of the trunk. It originates dorsally on the posterior edges of the tips of the ribs where the latter are free of the epaxial myomeres. Ventrally the majority of the fibers run deep to the *rectus abdominis* in a unique manner, but a few scattered fibers do extend over the *rectus abdominis*, especially immediately presacrally. In some places fibers attach to the anterior surface of one of the myocommata segmenting the *rectus abdominis*. The *o. e. superficialis* is not segmented by myocommata.

The *o. e. profundus* is deep to the unit just described. Even though its fibers parallel those of the *o. e. superficialis*, it remains distinguishable as a separate unit. The *o. e. profundus* blends dorsally with the intercostal musculature and ventrally it extends deep to the external flap of the *rectus abdominis*, ultimately blending with the latter. The *o. internus* is a distinct unit, underlapping the *subvertebralis* in the intercostal region. Ventrally it joins with the *o. e. profundus* to form the *rectus abdominis*. The fibers of the *o. internus* extend anteroventrally between the myocommata.

The most internal *transversus* differs in no significant way from that of *Taricha*. A distinct *rectus lateralis* extends between adjacent ribs, where the latter are free from the epaxial myomeres. Each segment of the *rectus lateralis* is overlapped anteriorly by a part of the *o. e. superficialis*. The *rectus abdominis* is also segmented by myocommata, between which the fibers proceed anteroposteriorly. A thin flap of the *rectus abdominis* extends dorsally over the *o. e. profundus* and ventralmost fibers of the *o. e. superficialis*.

Paramesotriton hongkongense (Myers and Leviton 1962)

RANGE. This species is found on the island of Hong Kong and the Kowloon region of the neighbouring coast of the People's Republic of China (Thorn 1968).

HABITAT. *P. hongkongense* is almost completely aquatic in small, slow-moving rivers, which have aquatic vegetation and a bottom of small rocks and stones under which they hide (Thorn 1968).

FOSSIL RECORD. None for the species or the genus.

RELATIONSHIPS. Bolkay (1928) classified *Paramesotriton chinensis*, the only species of the genus then named, in *Cynops*. On the basis of contact between the pterygoid and maxilla (either direct or cartilaginous), Chang (1935) related *Paramesotriton delousti* to *Pachytriton*, *Tylototriton*, and his new genus *Pingia* (= *Cynops orientalis*). In addition, he (1935) named a new genus *Trituroides* for *P. chinensis*, which he believed to be related to *Cynops* and *Hypselotriton*. Neither of Chang's genera are presently used.

Herre (1935b) saw a close relationship between *Paramesotriton* and *Cynops*, classifying the species of both genera in *Triturus*, but suggesting a closer alliance between them than either had with the other species of *Triturus*. Elsewhere, by recognizing the genus *Cynops* and continuing to place the species of *Paramesotriton* in *Triturus*, Herre (1939a) indicated a closer alliance of the latter two than of either to *Cynops*. Von Wahlert (1953) believed *Paramesotriton* to be close to the other newts of Asia, especially *Pachytriton*. By contrast, Freytag and Petzold (1961) concluded that *Paramesotriton*, although a member of the "higher" salamandrids, was not closely related to *Pachytriton*, but to the "Cynops-*ahnliche*" newts. It is to be noted that Wake and Özeti (1969, p. 135) have mistranslated the work of Freytag and Petzold (1961, p. 161), who state "*aber nicht mit* Pachytriton brevipes *in nähere genetische Beziehung gebracht werden kann.*" Wake and Özeti claim that these workers believed *Paramesotriton* to be close to *Pachytriton*, when in fact the opposite was argued.

Wake and Özeti (1969, p. 135) state that the hyobranchial apparatus of *Paramesotriton hongkongense* is more similar to that of *Triturus* than to that of *Cynops*, and that *Paramesotriton* is "more closely related to *Triturus* than to any other genus." Thorn (1968) considered *Paramesotriton* and *Cynops* to be close to the species of *Triturus* that Bolkay (1928) called "*Palaeotriton*", and that *Paramesotriton* was also allied to *Hypselotriton*. I group *Paramesotriton* with the other Asian newts (excluding *Tylototriton*) in the *Cynops* group (see Conclusions).

REMARKS. This species is large with a robust trunk and a long powerful tail. The limbs are large, but relatively less so than in *Taricha*. The trunk is relatively short, T13 generally bearing the pelvic girdle, and deep. There is a low, but distinct, crest extending down the back. This is formed by the high neural crests. The snout is pointed and the skull wide and very flat. The fronto-squamosal arch is large and completely bony.

Epaxial musculature (see Fig. 77).- The *dorsalis trunci* is developed as in *Cynops*, with short anterior flexures and powerful hyperapophyseal muscles. Large, roughened plates are present on the tops of the neural crests and extend above the epaxial musculature. The main bodies of the myomeres differ from those of *Cynops* in their greater lateral extent. The ribs do not reach beyond the *dorsalis trunci*, except for a very short projection in the immediate area of the pectoral girdle. There is no division of the column into the regions seen in *Cynops*. The amount of musculature in the epaxial myomeres is quite small.

Hypaxial musculature (see Fig. 77).- The *subvertebralis*, lying dorsal to the *transversus*, is composed of two layers of muscle fibers. These are not set off from each other, but are distinguishable owing to differences in the orientation of the fibers. Most ventrally, fibers originate on the anterior edge of one ventral lamella and extend anterolaterally to insert on the transverse process of the next anterior vertebra, at which point a small projection of bone is developed. Muscle fibers do not attach to the posterior edges of the ventral lamella, but extend above them. The anterolateral alignment of the ventral fibers is maintained laterally and ventrally, where the unit blends with the *o. internus*. Dorsal to this, the muscles of the *subvertebralis* extend anteroposteriorly between the transverse processes and posterolaterally between the ribs. The intercostal fibers become the *o. e. profundus* distal to the ribs.

The spinal nerves exit intravertebrally and pass laterally and then ventrally as in *Cynops*.

Lateral abdominal musculature (see Fig. 77).- The lateral abdominal musculature is extremely thin, but retains all the units described above in *Cynops pyrrhogaster*. The *o. e. superficialis* differs from that of *Cynops* in overlapping the *rectus abdominis* ventrally, thereby resembling the other newts. The *rectus lateralis* and simple *rectus abdominis* are constructed as in *Cynops*. The *o. e. profundus* is a separate unit, not being partially fused with the *o. e. superficialis* (contrast *Cynops*). It blends ventrally with the *o. internus* to form the *rectus abdominis*. The *o. internus* differs from the condition in *Cynops* in being continuous with the *subvertebralis* dorsally.

The *transversus* originates on the anterolateral and posterolateral borders of the ventral lamellae, a condition resembling that of *Siren*. A few stray fibers sometimes extend medially to the lateral edges of the centra under the anterior parts of the lamellae. There are large intercentral gaps in the *transversus*. Ventrally it is strongly attached to the *rectus abdominis*. Anteriorly, in the region of the shoulder girdle, a modified part of the *transversus* is found. This is a paired muscle, one part arising on either side of the vertebral column from the posterior septum of the fourth subvertebral myomere (counting the myomere spanning the atlas and the skull as number one). It then fans anteriorly to attach to the dorsal surface of the esophagus. A similar muscle is found in *Pleurodeles waltli*.

Triturus Rafinesque 1815

RANGE. Found throughout Europe west of the USSR, with species entering the USSR and the Middle East. Lacking from Ireland and northernmost Scandinavia (see Thorn 1968).

HABITAT. See under individual species accounts.

FOSSIL RECORD. Herre (1950) lists the following named species of fossil *Triturus*: *T. sansaniense* (Latret), from the Miocene of France; *T. lacasianum* (Latret), from the Miocene of France; *T. wintershofi* Lunau, from the Miocene of Germany. Estes and Hoffstetter (1976) consider *T. sansaniense* (Latret) to be *Salamandra sansaniense* Latret. Herre (1950, 1955) also named *Triturus schnaitheimi* from the middle Miocene of Germany and *T. roehrsi* from the Miocene of the Vienna Basin. Brame (1967) lists *T. megacephalus* Costa from the Cretaceous of Italy, but the validity of this species is questionable. Most recently, Estes and Hoffstetter (1976) reported on *Triturus* cf. *T. marmoratus* from the upper Miocene of France. Brunner (1956, 1957) referred parasphenoids from the German Pleistocene to *Triturus* species and *Triturus* aff. *marmoratus*.

Herre (1935b) notes that *Oligosemia* from the Oligocene of Spain and *Archaeotriton* from the Oligocene and Miocene of Czechoslovakia are *Triturus*-like. These genera may well by synonymous with *Triturus*.

RELATIONSHIPS. Noble (1931) included the North American and East Asian newts (excepting *Tylototriton*) in *Triturus*. Herre (1935b) considered *Triturus*, which he derived from *Taricha*, to be central to a large adaptive radiation. From it he derived the proteids, the sirenids, *Amphiuma*, *Notophthalmus*, *Neurergus*, and the Asian newts exclusive of *Tylototriton*. In agreement with previous workers, Wake and Özeti (1969) noted the close relationship of *Triturus* and *Neurergus*. They believed these two genera to be closest to the North American newts, and *Triturus* was stated to share characteristics of the hyobranchium with *Paramesotriton*. Salthe (1967) believed that courtship data indicated *Triturus* to be the most derived salamandrid.

Bolkay (1928) divided the species of *Triturus* into three species groups: *Palaeotriton*, *Mesotriton*, and *Neotriton*. Thorn (1968) updated these groups, which are based on cranial osteology, as follows:

Palaeotriton (strong frontosquamosal arch).

Content: *T. vulgaris** (type), *T. helveticus**, *T. vittatus**, *T. montandoni*, *T. italicus*, *T. boscai*.

Mesotriton (weakly developed frontosquamosal arch).

Content: *T. alpestris** (monotypic and very close to *Neurergus*).

Neotriton (frontosquamosal arch weak or absent).

Content: *T. cristatus** (type), *T. marmoratus**.

The species that are starred are described below.

Based on the structure of the frontosquamosal arch, the species that I studied can be placed in the following series: *T. cristatus* (arch lacking), *T. vittatus*, *T. alpestris*, *T. marmoratus*, *T. vulgaris*, and *T. helveticus* (complete bony arch). There are certain distinctions known in habitat and life history and these have been noted for each species. However, lacking detailed natural history observations, it is not possible to correlate structures with functions.

It is doubtful whether relationships within *Triturus* can be successfully elucidated at present. The three-way division presented above is, perhaps, an acceptable framework, although there are certain inconsistencies. *Triturus marmoratus* is not particularly like *T. cristatus* in terms of trunk musculature, but then neither is it greatly dissimilar. *T. alpestris* is very like the species of the *Palaeotriton* group (e.g., *T. vulgaris* and *T. vittatus*), with which it could be readily classified. In terms of the trunk musculature (and cranial osteology does not controvert this) *T. helveticus* is isolated from the other species, probably deserving of a separate group.

REMARKS. In certain species, notably *T. vulgaris* and *T. helveticus*, the ribs are long and extend far ventrally. This causes deformation of the lateral abdominal musculature when it is spread laterally for dissection. As a result, it has been difficult to represent the musculature exactly in the figures.

There is an apparent trend in *Triturus* towards close association of the epaxial musculature with the vertebrae and a decrease in the amount of musculature. This is reflected in the development of tall, robust neural crests and aliform processes. It is, however, probably more likely that the evolutionary trend is in the opposite direction, towards the re-development of large amounts of trunk musculature and less complex vertebrae. This would be the case if *Triturus* is as derived as most workers seem to believe (see Conclusions).

Triturus cristatus (Laurenti 1768)

RANGE. This species has an extensive range, being found through most of Europe, but absent from Ireland, Spain, Portugal, southwestern France, southern Italy, and southern Greece. It extends to "67°N in Scandinavia and to the extreme north of Scotland . . . . [In] France and in the Iberian Peninsula [it] is replaced by *Triturus marmoratus*.

. . . [*T. cristatus*] reaches well into Russia in the east of its range, while . . . further south [it] reaches as far east as Iran" (Steward 1969, p. 101).

HABITAT. "The Crested Newt is basically a lowland species . . . [and] might almost be regarded as a woodland species, since it is very much at home in deciduous woods though by no means confined to them." The distribution seems governed by the need for suitable breeding areas, as "it prefers fairly deep, weedy pools and during the daytime at least remains at greater depth than most other newts" (Steward 1969, pp. 101-102). Larvae are bottom dwellers, making extensive use of olfaction to find food. Adults are aquatic only during the breeding season, otherwise being found on land under logs, stones, and other surface debris (see Thorn 1968).

FOSSIL RECORD. None known for this species (see also under *Triturus* above).

RELATIONSHIPS. Bolkay (1928) grouped this species with *T. marmoratus* in *Neotriton* (see above discussion).

REMARKS. This is a large *Triturus*, reaching lengths of six inches or more total length. The trunk is heavy and relatively long, with 14 or 15 costal grooves in available specimens. The tail is short and laterally compressed. The limbs are large, but proportionally smaller and less robust than in other species of *Triturus*. There is a large amount of trunk musculature for a newt, although still less than in *Salamandra*.

Vertebrae are opisthocoelous, but the condyles are anteriorly flattened and barely fit into the posterior cotyles. In young, although fully metamorphosed individuals, amphicoely is still fully developed. This contrasts to the situation in most other newts, in which late larvae and postmetamorphic individuals are opisthocoelous. I interpret the reduction in the opisthocoelous condition and the simplification of the vertebrae to be secondary in *T. cristatus*, partially owing to paedomorphosis. All adult individuals dissected were in the aquatic, breeding phase.

Epaxial musculature (see Fig. 78).- The *dorsalis trunci* is massive, with a deep, narrow groove separating the two lateral halves. The anterior flexures are not differentiated from the main bodies of the myomeres as auxiliary units. Rather, each myomere slants slightly posteriorly, with the anterolateral face smoothly continuous from the main body to the anterior flexure. This is seen in certain other species of *Triturus*. In the forward regions of the column the anterior flexures extend to the hyperapophysis of the vertebra anterior to the pair spanned by their myomeres. In the posterior regions of the trunk, however, hyperapophyses are not met, the flexures extending only slightly beyond the transverse processes of the anterior vertebra of the pair spanned by a myomere. The anterior flexures are narrow, their medial parts hidden unless the myomeres are displaced laterally.

Muscle fibers extend anterolaterally in the main bodies of the myomeres. The *dorsalis trunci* does not extend beyond the tips of the ribs. In the area of the pectoral girdle the distal ends of the ribs serve as sites of origin for muscles leading to the suprascapula. Hyperapophyseal muscles are present and well developed, each originating over one half of the neural arch of one vertebra and inserting by a broad septum to the equivalent half of the hyperapophysis of the next anterior vertebra. Aliform processes are not present.

Hypaxial musculature (see Fig. 78).- The *subvertebralis* is underlain by the *transversus* and is otherwise conformable to the situation in other newts. Males especially, in the more anterior part of the column, have developed a small muscle that extends anteromedially from the lateral surface of the anterior part of one centrum to the posterior border of the ventral lamella of the next anterior vertebra (labelled as the transverse process muscle in Fig. 78). This unit is lacking from most of the column and even when present is a very indistinct part of the *subvertebralis*.

The ventral fibers of the *subvertebralis* extend anterolaterally between adjacent ribs, there being no underlap by muscle fibers beneath the ribs. Laterally this unit becomes the *obliquus internus*. Dorsal to this unit, the main mass of the intercostal musculature is composed of fibers extending anteroposteriorly between the ribs. This section is continuous with the *rectus lateralis* and also with the *o. e. profundus*.

Spinal nerves exit intravertebrally and then extend posterolaterally, exposed for much of their distance to the peritoneal cavity. At a point just below the distal ends of the ribs, each nerve passes external to the *transversus*, running between it and the *o. internus*.

Lateral abdominal musculature (see Fig. 78).- *T. cristatus* is foetal in its retention of four layers of musculature on the lateral body wall. Externally the *o. e. superficialis* is composed of fibers extending posteroventrally from their origin over the distal ends of the ribs to overlap the *rectus abdominis* ventrally. There is no dorsal overlap of the *dorsalis trunci*. In the more anterior regions of the trunk the *o. e. superficialis* is not segmented, but myocommata invade it posteriorly.

The *rectus lateralis* is located deep to the *o. e. superficialis*, just below the *dorsalis trunci*. The muscle fibers of this unit extend anteroposteriorly between, and also ventral to, the ends of the ribs. The *r. lateralis* is distinguishable owing to its greater thickness, but ventrally it blends into the *o. e. profundus*, the fibers of which run posteroventrally between the myocommata. Deep to this layer of the external oblique is the *o. internus*, which blends with the *o. e. profundus* ventrally to form the *rectus abdominis*. The latter is a simple, although thick, unit with fibers extending anteroposteriorly between myocommata.

The *transversus* originates along the lateral edges of the centra, without leaving intercentral gaps. The muscle fibers extend laterally and slightly anteriorly. In males there are about five myomeres located in the midtrunk region in which the subvertebral portion of the *transversus* is separated from the lateral abdominal part by myocommata. It is this area that has been figured (see Fig. 78). However, elsewhere along the column, and throughout the column in females available to me, the *transversus* is not interrupted by myocommata.

All of the layers of the lateral abdominal musculature are very thin. Except for the *r. lateralis* and the *r. abdominis*, each unit is composed of only a single layer of muscle fibers.

Triturus marmoratus (Latreille 1800)

RANGE. This species replaces its presumed relative *T. cristatus* in southeastern France, Spain, and Portugal. There is a broad area in central France where there is partial overlap of the two species and occasional hybridization occurs here (Steward 1969).

HABITAT. *T. marmoratus* is found in areas similar to those inhabited by *T. cristatus*, but in different regions (Thorn 1968). It is confined to lower altitudes and found on most sorts of soil, although breeding sites appear to dictate the distribution. "Running water is normally avoided and it prefers small but reasonably deep ponds, pools, and ditches, especially where there is an abundance of water-vegetation" (Steward 1969, p. 115). Except during the breeding season, adults are terrestrial.

FOSSIL RECORD. Brunner (1957) referred a parasphenoid from the Pleistocene of Germany to *Triturus* aff. *marmoratus*, and Estes and Hoffstetter (1976) describe material of *Triturus* cf. *T. marmoratus* from the Miocene of France.

RELATIONSHIPS. This species is grouped with *T. cristatus* in the *Neotriton* group (see above).

REMARKS. The body proportions are very like those of *T. cristatus*. Both are relatively large, with long robust trunks and relatively long, laterally compressed tails. The limbs are fairly large, but relatively less so than in other species of the genus (e.g., *T. helveticus* and *T. vulgaris*). There are 10 or 11 myomeres between the limb girdles. Vertebrae differ from those of *T. cristatus* in having fairly tall, robust neural crests, and distinct ventral lamellae. The amount of trunk musculature is relatively small, and the lateral abdominal musculature is extremely thin.

Epaxial musculature (see Fig. 79).- The shape of the myomeres of the *dorsalis trunci* differ from those of *T. cristatus*. With the presence of high, plate-like neural crests and small aliform processes, *T. marmoratus* differs from *T. cristatus*, but is more like most other newts. The tops of the neural crests are not covered by musculature, the *dorsalis trunci* being disposed laterally on either side. There is no development of capping plates on the neural crests.

Anterior flexures are short and relatively narrow, extending a very short distance beyond the aliform process of the anterior vertebra of the pair spanned by the myomere. A short septum extends forward from the apex of each anterior flexure. The anterior myoseptum of each myomere rises posteriorly, is smoothly continuous between the main body and the associated anterior flexure, and is gently concave posteromedially. The main bodies of the myomeres are of relatively small mass, but are developed as those of *T. cristatus* and lack the extreme modifications of certain other newts (e.g., *Euproctus* and *Salamandrina*). Laterally each myomere ends a significant distance before the distal ends of the ribs that it spans.

The lateral edges of each aliform process give rise to posteriorly directed hyperapophyseal septa, one per arm of the process. Muscle fibers extend posterolaterally to the septum from the next posterior anterior flexure, and posteromedially to the neural crest of the next posterior vertebra. The hyperapophyseal septum is oriented vertically. In superficial view these muscles are not visible, being covered by a layer of muscle fibers extending anteroposteriorly in the medial part of each anterior flexure.

Hypaxial musculature (see Fig. 79).- The *subvertebralis* is constructed as in *T. cristatus* and is also underlain by the *transversus*. Medially the subvertebral fibers run anteroposteriorly between the borders of adjacent pairs of ventral lamellae. Lateral to the transverse processes, beneath adjacent ribs, the fibers come to extend anterolaterally. This unit proceeds laterally and ventrally without break to form the *obliquus internus*. Dorsal to this thin layer, between the ribs, the intercostal musculature extends anteroposteriorly. This unit blends with the *rectus lateralis* distally. The *subvertebralis* is segmented into simple, discrete myomeres, each one extending between only two vertebrae, and no flexures are developed.

Spinal nerves exit intravertebrally through the walls of the neural arches, just posterior to the origins of the transverse processes. Each nerve is exposed to the peritoneal cavity for much of its distance, lying external to the *transversus* for only a short way in the area of the transverse processes. Ventrally, not far from the lateral edge of the *rectus abdominis*, the nerves extend between the *transversus* and the *o. internus*.

Lateral abdominal musculature (see Fig. 79).- Except for the *rectus lateralis* and parts of the *rectus abdominis*, the lateral abdominal musculature is very thin. There is only a single layer of fibers in the *obliquus externus*. Based on fibral orientations and positional relationships, this is probably homologous to the *o. e. superficialis* of other salamanders. The fibers of this unit extend ventrally and slightly posteriorly and are not divided by myocommata. Dorsally the fibers converge to originate on the distal ends of the ribs. Ventrally the unit overlaps the *rectus abdominis* to a limited extent.

Ventral to the *dorsalis trunci* and running between adjacent ribs is the *rectus lateralis*, which is a direct continuation of the intercostal series. Much of the *rectus lateralis* is exposed laterally, owing to the origin of the *o. e. superficialis* on the ribs rather than over the epaxial musculature. There is no trace of an *o. e. profundus*, the *o. internus* lying deep to the *o. e. superficialis*. This middle layer is composed of fibers extending anteroventrally between the myocommata. Ventrally the *o. internus* forms part of the *rectus abdominis*, the fibers here being oriented anteromedially.

The most internal *transversus* arises medially and dorsally along the lateral edges of the centra and is not segmented by myocommata at any point. Ventrally it inserts on the internal, lateral edge of the *r. a. superficialis*. The *rectus abdominis* is divided into two parts, here termed the *r. a. superficialis* and the *r. a. profundus*, although homologies are not certain. The two units are located side-by-side as in *Salamandra* and do not show the arrangement present in *Salamandrina*, *Tylototriton*, and salamanders of more primitive families. The *r. a.*

superficialis is thin, segmented by myocommata, and composed of fibers extending anteroposteriorly. Lateral to it, and of approximately equal width, is the *r. a. profundus*. This unit is itself composed of two parts: a superficial part with fibers extending anteroposteriorly, and a deeper unit with fibers running anteromedially. The deeper part is a direct continuation of the *o. internus* and, therefore, perhaps not properly a part of the *rectus abdominis*. Nevertheless, the double layered nature of the *r. a. profundus*, with fibers running in two slightly different directions, is similar to the condition seen in *Salamandrina*, *Tylototriton*, plethodontids, and some hynobiids. However, in *T. marmoratus*, the *r. a. profundus* is tightly bound to the *r. a. superficialis* and is not free.

Triturus alpestris (Laurenti 1768)

RANGE. The species has an extensive distribution in Europe, being found eastwards from northern and central France and northern Italy, and extending into the USSR and the Balkans. There is also a single isolated population in northern Spain about Lake Evcina (Thorn 1968, Steward 1969).

HABITAT. This is largely, but not exclusively, an inhabitant of higher altitudes. It is very tolerant of low temperatures and is found either on land or in the water of mountain lakes, ponds, and slowly moving streams. Nocturnal and crepuscular when on land, it is active during lighter periods than other *Triturus*. Highly mobile, *T. alpestris* wanders over land and in the water throughout the year. "In the water, these newts are bottom dwellers rather than free swimmers", being found in both shallow and deep water (Steward 1969, p. 95). Neoteny is relatively common.

FOSSIL RECORD. None for this species; that of the genus is discussed above.

RELATIONSHIPS. *T. alpestris* is often classified in its own group in the genus *Triturus*, but it is probably more properly to be included with *T. vulgaris*, *T. vittatus*, and their allies in the *Palaeotriton* group (see Bolkay 1928, Thorn 1968, also above).

REMARKS. This is a medium-sized member of the genus *Triturus*. The trunk is relatively robust and the tail quite short. The limbs are small, but well developed.

Epaxial musculature (see Fig. 80).- The *dorsalis trunci* is so similar to that of *T. vittatus* (q.v.) as to require no additional description.

Hypaxial musculature (see Fig. 80).- The *subvertebralis* differs in no discernable way from that of *T. vittatus* (q.v.).

Lateral abdominal musculature (see Fig. 80.).- This complex is also developed more or less as in *T. vittatus*, but with certain distinctions. The *transversus* differs in having intercentral gaps, as in *T. vulgaris*. The spinal nerves are exposed to the peritoneal cavity for a somewhat shorter distance than in *T. vittatus*. The *o. e. profundus* and *o. internus* are extremely thin layers, each being composed of semi-isolated, individual muscle fibers extending between adjacent myocommata. Together they form somewhat of a latticework between the *transversus* and *o. e. superficialis*.

Triturus vittatus (Jenyns 1835)

RANGE. According to Thorn (1968), this species has a disjunct distribution, one group found along the southern and eastern coasts of the Black Sea in Asia Minor. From the east coast the range extends eastwards almost to the Caspian Sea. The second group is found along the Mediterranean coasts of Lebanon and Israel, extending into Syria and Iraq.

HABITAT. The northern subspecies (*T. vittatus ophryticus*) is a mountain dweller of cold lakes, ponds, and slower streams. The southern subspecies (*T. v. vittatus*) inhabits lower regions close to or in temporary ponds with little aquatic vegetation, but with large numbers of crustaceans and insects. It is less common in rivers. The species is apparently highly aquatic, though not exclusively so (see Thorn 1968, Steward 1969).

FOSSIL RECORD. None for this species; that of the genus is discussed above.

RELATIONSHIPS. *T. vittatus* is classified with *T. vulgaris*, *T. helveticus*, and others in the informal *Palaeotriton* group (see Thorn 1968). It is very similar to *T. vulgaris* and *T. alpestris* in terms of trunk musculature, but differs rather markedly from *T. helveticus*.

REMARKS. The trunk is relatively slender and more or less cylindrical. Costal grooves are not distinct, but there are 10 or 11 myomeres between the pectoral and pelvic girdles. The tail is relatively short and laterally compressed. Limbs are thin and not overly long. Although a bony frontosquamosal arch is not present in any of my specimens, Bolkay

(1928) figures a thin but complete bony arch in a male of this species. There is, therefore, presumably variation in this feature.

Epaxial musculature (see Fig. 81).- The *dorsalis trunci* is not massive, the amount being much less than that found in *T. cristatus*. The epaxial myomeres are narrow and in close association with the vertebrae, especially the neural crests, aliform processes, and transverse processes. Ribs extend beyond the lateral borders of the *dorsalis trunci* for approximately one third their total length. The myomeres slant very slightly posterodorsally from between adjacent vertebrae. The tops of the neural crests and aliform processes are not buried beneath musculature. Rather, each myomere extends laterally from the top edge of its associated neural crest.

The anterior flexures are relatively narrow and very short. Medially, each generally attaches to the anterolateral edge of one of the sides of an aliform process. A septum extends anteriorly from the apex of each flexure. In the anterior portion of the trunk these septa appear to join the posteromedial edge of the main body of the next anterior myomere. In the more posterior region the septa proceed only a short distance beyond their anterior flexures. The forward attachments of these septa are problematical. Each septum is extremely thin anteriorly, but it does appear to attach to the next anterior myoseptum in places.

Fibers extend anterolaterally in the main bodies of the myomeres, forming long tracts along the vertebral column. As in *T. cristatus* and others, the main body and the anterior flexure of each myomere are a single coherent unit, with the anterior, bounding myoseptum extending smoothly between the two parts. Hyperapophyseal muscles are present and well developed throughout the trunk. They are overlain by a thin layer of muscle fibers running between adjacent aliform processes in the anterior flexures. In a manner very similar to that found in *Siren*, each aliform process gives rise to two vertical septa, each extending posteriorly from one of the lateral edges. Each septum gives rise to fibers that run posteromedially and posterolaterally to the paralleling neural crest and septum of the associated anterior flexure. This organization is almost certainly apomorphic, indicating close relationship between *Siren* and the salamandrid newts.

Hypaxial musculature (see Fig. 81).- The *subvertebralis* is as in other newts, exhibiting a condition somewhat different from that of *T. cristatus* and *T. marmoratus*. The *transversus* underlies the *subvertebralis*, originating along the centra. When this thin layer is removed, the simple *subvertebralis* is evident. The most ventral layer extends anteroposteriorly between adjacent ventral lamella and ribs. The ventral lamellae are not underlain by subvertebral musculature, except for the *transversus*, and serve as areas for the deposition of fatty tissue in addition to their function in locomotion. Distal portions of the ribs are completely covered ventrally by the *subvertebralis*.

The *obliquus internus* invades the subvertebral area, extending medially under the *subvertebralis* to about the midpoint of the ribs. Above this, the subvertebral fibers proceed anteroposteriorly. Dorsal to the anteroposterior unit, muscle fibers run in different directions. The anterior edge of each ventral lamella gives rise to muscle fibers that extend anterolaterally, converging on the distal edge of the ventral rib-bearer of the next anterior vertebra. A short, broad spike of bone often projects posteromedially from the rib-bearer to serve as an area of insertion for these muscles. Intercostally, muscle fibers run posterolaterally. This group proceeds laterally and ventrally beyond the ribs to form the *o. e. profundus*.

Spinal nerves exit intravertebrally and extend laterally along the inner surface of the *transversus* just posterior to the associated rib and myoseptum. Ventrally each nerve comes to lie along a myocomma between the *transversus* and *o. internus*.

Lateral abdominal musculature (see Fig. 81).- The muscle layers about the lateral and ventral walls of the body are extremely thin, each composed of only a single layer of fibers. Nevertheless, all four layers are present laterally. The *o. e. superficialis* lacks myoseptal divisions and originates at points over the distal ends of the ribs. A thin fascia attaches to the tips of the ribs and the muscle fibers converge on these areas, allowing the *o. e. superficialis* to act directly on the individual ribs. The *o. e. superficialis* is relatively narrow, barely reaching the *rectus abdominis* ventrally.

Much of the *rectus lateralis* is not covered by the *o. e. superficialis*. This band is thin and completely intercostal. Beneath the two layers just described is the *o. e. profundus*. This is segmented by myocommata and its fibers extend posteroventrally. It is a direct continuation of the *subvertebralis* and blends imperceptibly with the *rectus abdominis* ventrally. The *o. internus* lies deep to the *o. e. profundus*. This unit has separated from the *subvertebralis*, which it underlies. The fibers of the *o. internus* extend anteroventrally and come to underlap the *rectus abdominis* ventrally. There is some slight intergradation with the *rectus abdominis*, but the two units are essentially distinct.

The *transversus* originates along the centra as in other newts. Its fibers run anterolaterally and then anteroventrally from there. In the region of the midtrunk, a part of the *transversus* is bound to the subcostal myosepta. However, excepting this, there are no segmenting septa. The *transversus* is applied against the inner surface of the *rectus abdominis* ventrally, terminating along a line approximately two thirds of the width of the latter. The *rectus abdominis* is a simple ventral continuation of the *o. e. profundus*. It is segmented by myocommata and its fibers extend anteroposteriorly.

Triturus vulgaris (Linnaeus 1758)

RANGE. This is the most wide-ranging species of *Triturus*, found throughout the British Isles and Ireland, far north into Norway and Sweden, and east to the Urals in the USSR. In the south it extends throughout Italy, the Balkans, and the Greek peninsula, then east along the south coast of the Black Sea and well into the southern Caucasus. It is lacking from France, Switzerland, and the whole of the Iberian peninsula, where is is replaced by *T. boscai* (see Steward 1969).

HABITAT. It is found in "wooded and open areas, mountains and plains . . . and almost any kind of standing water, from temporary pools to the margins of lakes, can serve for breeding" (Steward 1969, p. 123).

Generally, however, *T. vulgaris* is restricted to lowlands. Correlated with this habitat diversity, "size, colour, and pattern vary considerably over the total range" (Steward 1969, p. 123). It is an active wanderer and colonizer of new ponds. The adults are terrestrial throughout the year, except during the breeding season and even during this time they frequently leave the water at night. The larva is free-swimming, relying on "eyesight [in hunting] and frequently 'hawks' after small insects in mid-water or at the surface" (Steward 1969, p. 128).

FOSSIL RECORD. None for this species; that of the genus is discussed above.

RELATIONSHIPS. This is the type species of Bolkay's (1928) *Palaeotriton* group (see Thorn 1968), which also includes *T. vittatus* and *T. helveticus*, and to which I would add *T. alpestris*.

REMARKS. These are small newts with robust limbs and a body of typical *Triturus* proportions. There are 10 or 11 myomeres between the limb girdles. There is a relatively small amount of trunk musculature, the *dorsalis trunci* being concentrated next to the column and the ribs extending down into the lateral abdominal musculature.

Epaxial musculature (see Figs. 82 and 83).- The *dorsalis trunci* is developed as in *T. vittatus*, but the anterior flexures appear to extend forward a lesser distance in *T. vulgaris*.

Hypaxial musculature (see Fig. 82).- The condition is almost identical to that of *T. vittatus* and *T. alpestris*, but ventral lamellae are much more strongly developed in *T. vulgaris*. The *transversus* attaches to the centra, leaving a large gap at the level of each intercentral joint.

Lateral abdominal musculature (see Figs. 82 and 83).- Except for the fact that *T. vulgaris* has both the *o. e. profundus* and *o. internus* blending ventrally to form the *rectus abdominis*, the lateral abdominal musculature is as in *T. vittatus* and *T. alpestris*. Maurer (1911), pl. 6, fig. 14) figures a separate *r. a. superficialis* for this species (as *Triton taeniatus*), but I find no such differentiation in my specimens.

Triturus helveticus (Razoumowsky 1789)

RANGE. This species is found throughout the British Isles, except for Ireland, and is absent from the southern half of the Iberian peninsula. It is otherwise "confined to Western Europe, extending eastwards only approximately as far as a line drawn southwards from Hamburg in Germany" (Steward 1969, p. 111).

HABITAT. *T. helveticus* is similar in habits and habitus to *T. vulgaris*, but "favours hilly or mountainous regions and is less at home at low levels . . . . [It] is generally more often found on sandy, peaty, or limestone soils than on clay or alluvium" (Steward 1969, p. 111). It is terrestrial except during the breeding season, when shallows of ponds, lakes, and slow streams are invaded. *T. helveticus* prefers a muddy substrate and abundant water vegetation. On land prey is usually small and captured with the protrusible tongue, although larger prey is seized in the jaws. In spite of Thorn's (1968) claim that it is highly aquatic, it does not have a "water-tongue".

FOSSIL RECORD. None for this species; that of the genus is discussed above.

RELATIONSHIPS. Although grouped with *T. vulgaris*, *T. vittatus*, and others in the *Palaeotriton* group (see Bolkay 1928, Thorn 1968), it would probably be better to isolate *T. helveticus* in its own group, as its trunk musculature is so distinctly different from that of the other species of *Triturus* described here.

REMARKS. These are very small newts, with an individual of 10 cm total length being large. The limbs are relatively long and robust, the trunk is short and thin. The tail is thin and somewhat laterally compressed. The ribs are very long, and extend much further ventrally than is usual in salamanders.

Only two small specimens were available for dissection (snout-vent lengths of 32 and 36 mm). Owing to this, and to the very small amount of musculature present in the trunk, certainty as to exact locations of the myomeres (especially the epaxial) is not complete. Modification of certain observations may be necessary upon further study.

Epaxial musculature (see Fig. 84).- The *dorsalis trunci* differs from that of the other species of *Triturus*. The amount of musculature is small and the myomeres extend just beyond the midpoints of the bony parts of the ribs. Anterior flexures are suppressed to the extent of not being clearly separable from the main bodies of the myomeres. The anterior septum of the main body of each myomere sweeps gently forward to attach to the aliform process and posterior zygapophysis of the next anterior vertebra. There is slight anteroventral orientation of the muscle fibers in the main body of each myomere.

The hyperapophyseal muscles are well developed, with a vertical septum extending posteriorly from each wing of the aliform process forming their centres. Muscle fibers extend posteromedially and posterolaterally from these septa. The myosepta extend down the front of the ribs in the main bodies of the myomeres, an unusual situation in salamanders.

Hypaxial musculature (see Fig. 84).- As in other newts the *subvertebralis* is underlain by the *transversus*. Each muscle block extends between two vertebrae and their associated ribs. The ventral lamellae are very robust, more similar to those of the Asian and North American genera than to those of the other species of *Triturus*. Fibers extend anteroposteriorly between these lamellae. Beyond the ventral lamellae, between the ribs, the fibers extend posterolaterally. Most distally, the fibers of this layer run posteroventrally from the tip of the bony portion of each rib to the anterior edge of the cartilaginous tip of the next posterior rib.

The second, more dorsal, layer of the *subvertebralis* may be subdivided into two areas. Medially the fibers originate on the anterior surface of each ventral lamella and then converge anteriorly to insert on the posterior surface of the next anterior dorsal rib-bearer. At the point of insertion a bony spike is often developed. More laterally, between the ribs, the intercostal fibers run anteroposteriorly. This latter unit becomes the *rectus lateralis* where the ribs extend beyond the *dorsalis trunci*.

The spinal nerves are basically as in *T. vulgaris*.

Lateral abdominal musculature (see Fig. 84).- A large part of each rib is incorporated into the lateral abdominal musculature. The *rectus lateralis* consists of those fibers extending anteroposteriorly between the ribs and ventral to the *dorsalis trunci*. The *obliquus externus* (?*o. e. superficialis*) originates dorsally on the posterior surfaces of the cartilaginous tips of the ribs. From each point of origin fibers fan posteroventrally to insert on the external surface of the *rectus abdominis*. The *o. externus* is not divided by myocommata. There is no trace of an *o. internus*, the *transversus* being directly applied against the *o. externus*.

The *transversus* originates along the edges of the centra, but leaves intercentral gaps. The *transversus* extends ventrolaterally from the centra, with a very slight anterior component to this orientation. Where it underlies the ribs the *transversus* is attached to their inner surfaces. Ventrally it joins to the inner surface of the *rectus abdominis*. As neither the *o. externus* nor the *transversus* are segmented by myocommata, the lateral body musculature is composed of two thin sheets of undivided muscle, a condition quite similar to that seen in lizards. The *rectus abdominis* is a pair of simple longitudinal bands situated ventromedially. It is bound to the *transversus* and *o. externus* of either side, but does not blend with either. It is segmented by myocommata and is relatively thick.

Euproctus asper (Dugès 1852)

RANGE. The species is found only in the Pyrenees of Spain, Andorra, and southwestern France. Of the other species of *Euproctus*, *E. montanus* is found on the island of Corsica and *E. platycephalus* on Sardinia (Steward 1969).

HABITAT. Confined to higher altitudes, *E. asper* is adapted to low temperatures, being found in mountain rivers and streams where it is generally benthic. In correlation with this life style, the lungs are greatly reduced. This newt breeds in water "among rocks at the edges of streams and lakes" (Steward 1969, p. 75, also Thorn 1968).

FOSSIL RECORD. None known for the species or the genus.

RELATIONSHIPS. Boulenger (1917) suggested that *Euproctus* was possibly triphyletic and closely related to "*Rhithrotriton*" (= *Neurergus crocatus*), from which it probably originated. Bolkay (1928), although suggesting that ambystomatids and salamandrids were derived from a common ancestor, believed *Euproctus* to have originated from this ancestral stock prior to the divergence of the two families. A close relationship of *Euproctus* with *Pachytriton* and amphiumids was indicated by Herre (1935b).

Noble (1931) believed *Euproctus* to have been derived from a stock in common with *Triturus*, *Pleurodeles*, and *Pachytriton*, which in turn evolved from some species of *Tylototriton*. Arguing that the courtship "pattern of *Euproctus* itself may be a slightly modified form of the ancestral pattern of the salamandrids," Salthe (1967, p. 108) suggested that the genus originated from primitive salamandrid stock. There is actually no reason to consider the courtship of *Euproctus* to be particularly primitive. In this genus the male captures the female with his tail, which is unique amongst the Salamandridae. It is more likely that the courtship of the Salamandrinae and Pleurodelini is primitive for this family and that that of *Euproctus* developed secondarily from the sort seen in *Triturus*. It is more reasonable that capture with the tail would have developed from an ancestor lacking capture, rather than being modified from the primitive pattern of capture with the forelimbs. *Euproctus* is probably a highly derived member of the Triturini (see also Salthe and Mecham 1974).

REMARKS. The trunk is relatively long, although it has only 12 myomeres between the limb girdles. The tail is long, heavy, and not notably compressed laterally. The amount of trunk musculature is reduced in comparison to most other newts. The limbs are relatively robust, and the head is markedly flattened and posteriorly widened. In *E. asper* a well-developed bony frontosquamosal arch is present. According to Thorn (1968), *E. platycephalus* has a complete bony arch, but Bolkay (1928) figures a specimen of this species (as *E. rusconii*) in which the arch is not quite complete. Thorn (1968) describes *E. montanus* as having an incomplete bony arch formed largely by a ligament. Bolkay (1928), however, figures a specimen in which there is no trace of the bony processes for attachment of the frontosquamosal ligament. It is likely that there is intraspecific variation in this feature.

It is claimed (Steward 1969) that *Euproctus* is intolerant of any but low temperatures, but in 1976 I maintained two specimens of *E. asper* at room temperature (22°C) for over two months prior to their being sacrificed for dissection. During this time they were extremely active and fed readily. The female spent much time out of water, whereas the male remained in the water. The higher than normal temperature seemed to have no harmful effects, the specimens remaining healthy and hungry. Steward (1969, p. 76) describes the adults as "in general slow-moving and sluggish, whether in water or on land . . . [and] incapable of catching anything other than slow-moving prey like earthworms and slugs, and, in the water, such grubs and other larvae as are found under the stones where the salamanders also spend much of their time." However, at least under laboratory conditions, *E. asper* is extremely active and quick, feeding readily on rapidly moving water invertebrates (e.g., the crustacean *Gammarus*). Feeding is similar to that observed in captive *Cynops* and *Notophthalmus*: the salamander moves slowly towards a moving prey item and then makes a quick forward lunge, while opening the mouth and depressing the hyobranchium. Although sometimes inaccurate, *Euproctus* is no more "slow-moving" or "sluggish" than *Taricha*, *Cynops*, *Notophthalmus*, or *Ambystoma* under laboratory conditions.

Epaxial musculature (see Figs. 85 and 86).- Only a very thin layer of epaxial musculature covers the vertebrae. Owing to the small mass of the *dorsalis trunci*, the myomeres cannot be said to be inclined posteriorly. Rather, they overlap in a manner similar to shingles. The anterior flexures are very short and broad, a septum extending forward a variable distance from each apex. The neural crests and aliform processes are covered dorsally by a thin layer of muscle fibers.

A vertical septum extends posteriorly from each wing of the aliform process. Muscle fibers insert on the aliform process and its septum and extend posteriorly. They originate along the lateral edge of the neural crest, the front of the aliform process, the roof of the neural arch, and the top of the transverse process of the following vertebra. In addition, some fibers arise from the internal surface of the septum extending from the anterior flexure of the associated myomere and extend to the hyperapophyseal septum.

The main body of each epaxial myomere ends laterally at a line extending approximately through the midpoints of the ribs. Muscle fibers extend anteriorly and slightly laterally in this portion of the *dorsalis trunci*. The ribs are very long and robust for a salamander, curving ventrally beneath the *dorsalis trunci*.

Hypaxial musculature (see Fig. 85).- The *subvertebralis*, underlain by the *transversus*, is composed of a single unit of fibers. These fibers extend anteroposteriorly between the transverse processes and posterolaterally between the ribs. The *subvertebralis* does not extend under the ribs or transverse processes to cover them ventrally. The spinal nerves are thick, exit intravertebrally, and are associated with the muscle units laterally and ventrally as in other newts generally.

Lateral abdominal musculature (see Fig. 86).- The *o. e. superficialis* originates serially along the posterior edges of the ribs and then extends posteroventrally to overlap the *rectus abdominis*. The *rectus lateralis* extends between the ribs, deep to the *o. e. superficialis*, and is continuous with the fibers of the intercostal series. The *o. e. profundus* lies internal to the *o. e. superficialis*. Unlike the latter unit, it is divided by myocommata and its fibers extend posteroventrally at a lesser angle than those of the *o. e. superficialis*. Dorsally the *o. e. profundus* is continuous with the *subvertebralis* and it blends ventrally with the *rectus abdominis*. There is no trace of an *o. internus*.

As in *Triturus*, the *transversus* originates along the lateral edges of the centra. Relatively long, but narrow, intercentral gaps are present. The muscle fibers of the *transversus* extend anterolaterally and then anteroventrally at a very acute angle to the vertebral column, differing from *Triturus* in this regard. The *transversus* is applied against the internal surface of the *o. e. profundus* and partially underlies the *rectus abdominis* ventrally. The latter is a single, simple unit with fibers extending anteroposteriorly between the myocommata. It is formed by a ventral extension of the *o. e. profundus*, but also overlaps the latter with a thin flap of musculature externally.

viii) Family Sirenidae Gray 1825

Siren Linnaeus 1766

Siren lacertina Linnaeus 1766

Siren intermedia LeConte *in* Harlan 1827

RANGE. "The Coastal Plain of [the] southeastern United States from the District of Columbia to Florida and westward in the Gulf states to extreme northeastern Mexico. In the Mississippi Valley, they range northward through Illinois and Indiana to southwestern Michigan" (Martof 1974, p. 152.1).

HABITAT. *Siren intermedia intermedia* is found in "cypress and pinewoods ponds and ditches, where they hide by day beneath bottom vegetation and stranded logs" (Bishop 1943, p. 458). *S. intermedia nettingi* is "found in mucky and muddy ditches, sloughs, and flatlands ponds" (Bishop 1943, p. 461). *Siren lacertina* is known from "shallow roadside ditches, from beneath rocks in the bed of a swift-running stream, from weedy ponds and pools and muddy swamps" and it is especially common in "weed-choked and mud-bottomed" lakes (Bishop 1943, p. 464). *Siren* is capable of estivation in the mud of dried-up ponds and can move short distances over land.

FOSSIL RECORD. *S. lacertina* is known from the Pleistocene of Florida (Lynch 1965). The genus *Habrosaurus* is known from the Upper Cretaceous (Estes 1964) and Paleocene (Estes 1976) of North America, and is unquestionably a sirenid. *Siren dunni* has been named from the Eocene of Wyoming (Goin and Auffenberg 1957). *Siren hesterna* is from the Miocene and *S. simpsoni* from the Pliocene of Florida (Goin and Auffenberg 1955). Fossils referable to *Pseudobranchus* have also been discovered in the Tertiary of North America (Goin and Auffenberg 1955). The fossil species of *Siren* and *Pseudobranchus* are little different from the living ones.

RELATIONSHIPS. Numerous phylogenetic schemes and hypotheses of relationship have been put forth regarding the sirenids. Details of these are discussed below in the Conclusions. It may be said here that sirenids are closely related to the Salamandridae and to be classified within the Salamandroidea.

REMARKS. Although no trace of the pelvic limbs or girdle remains, the anterior limbs are present. These are relatively small, but robust and much used in swimming, burrowing, and moving over the substrate. These animals are active and powerful burrowers, tunneling through gravel and under rocks in aquaria. They often lie with only the head and gills exposed above the surface of the bottom, lunging forward to capture passing prey.

The trunk is long, deep, and robust, with 30 to 40 costal grooves. A large mass of musculature surrounds the vertebral column, especially in larger individuals of *Siren lacertina*. The lateral abdominal musculature is also very thick. As indicated by their shape, these animals are relatively slow but powerful swimmers.

Epaxial musculature (see Figs. 87, 88, and 89).- The *dorsalis trunci* is of salamandrid-like plan, but modified. The surrounding skin is tough and tightly bound to the trunk musculature by connective tissue. Auffenberg (1959, p. 255) misinterpreted this area, believing that muscle fibers from the *dorsalis trunci* extended out to the skin ("Fibers from this division extend out distally to all parts of the dorsal area and attach to the inner surface of the skin, making it somewhat difficult to remove"). These are not muscle fibers at all, but as previously noted by Maurer (1892, p. 92) "*eine sehr derbe subcutane Fascie.*"

Auffenberg (1962, p. 185) states: "The most complex [epaxial] intervertebral system is found in the genus *Siren*. Examples of this complexity are found in the fiber tracts running from the prezygapophyseal processes of one vertebra, to the postzygapophyseal processes of an adjacent vertebra, and the tracts running from the transverse process of one vertebra to the postzygapophyseal process of another vertebra." These statements are misleading, in that the more intimate connection of muscle fibers with the vertebrae might give a superficial appearance of greater complexity (but see *Amphiuma*). However, in larger view, considering the functional units of the *dorsalis trunci* (the myomeres), *Siren* is less complex than many other salamanders. Even the muscles extending back from the aliform processes are merely slightly enlarged hyperapophyseal muscles seen also in salamandrids.

The anterior flexures are relatively short and narrow, not being distinctly set off from the main bodies of the myomeres (compare the Triturini). The myoseptum of each attaches to the edge of the neural crest, extending posterolaterally along the top of the aliform process. At the posterior end of the aliform process it extends along the interzygapophyseal crest (see Fig. 1E) to the top of the third alar process. The septum attaches along the third alar, running into the myomere distal to the tip of the transverse process.

The main body of the myomere is strongly inclined posteriorly, such that each myomere extends posterolaterally from between adjacent vertebrae. Unlike the other anguilliform urodele, *Amphiuma*, *Siren* has not developed enlarged or auxiliary flexures, but retains a relatively simple *dorsalis trunci*. The modifications involve an increased posterolateral extension of the main bodies of the myomeres. The muscle fibers within the epaxial mass are largely parallel to the vertebral column.

It is sometimes stated (e.g., Auffenberg 1959) that the aliform process is unique to sirenids. However, as noted by Estes (1964, 1965b), this is not true. *Siren* has merely accentuated the aliform process already present in newts. The hyperapophyseal muscles associated with these processes are developed as in the newts (q.v.). Auffenberg (1959) divided the muscle fibers associated with the aliform processes and the septa into three tracts: IV-1, IV-2, and IV-3.

He states (p. 259) that: "The fibers of . . . [the IV-1] series begin near the medio-anterior dorsal surface of the projected anterior upper edge of the neural arch. The fibers thence continue anteriorly, connecting to the posterior surface of the entire length of each of the arms of the V-shaped aliform processes . . . . In action the tract must be similar to the multifidus muscle of some of the reptiles with a posteriorly extended neural arch, as is found in the snakes. There is no reason to suppose that these units are homologous [, however]." Auffenberg's IV-2 tract is composed of those fibers associated directly with the hyperapophyseal septum (the latter not recognized by him). Fibers proceed from each septum in several directions. Medially fibers extend posteromedially from the septum to the neural crest and aliform process of the next posterior vertebra. Laterally the fibers run posterolaterally and ventrally to the surface of the neural arch of the next posterior vertebra. Auffenberg (1959, p. 259) states of this unit that "in action it must be very similar to the intervertebralis of higher vertebrates and is probably a true homologue of this [latter] muscle." Regardless of the functional relationships, phylogenetic homology is extremely doubtful.

Auffenberg's IV-3 series of muscle fibers "originate on the prezygapophysis of the next posterior vertebra, to insert with the fibers of IV-2 on the aliform process" (p. 260). In fact, these fibers insert onto the hyperapophyseal septum. I suggest that it is artificial to distinguish these three series, which only adds confusion and obscures functional and phylogenetic relationships. Rather, the complex is here called the hyperapophyseal muscle, as done above for salamanders of other families. Of Auffenberg's other intervertebral tracts, I am unable to find the one termed IV-4, whereas IV-5 simply extends between adjacent transverse processes. As noted elsewhere, the utility of distinguishing numerous intervertebral, interseptal, and septal-vertebral fiber tracts is doubtful, and Auffenberg's terminology is not followed.

Auffenberg (1959, p. 254) inferred that "the unusual vertebral processes of the Sirenidae suggest that the epaxial muscle fiber tracts are probably more complex than those of most other living urodeles." First of all, the vertebral structure of sirenids is not really "unusual" (compare the newts), and secondly, the musculature is not more complex (compare cryptobranchoids, amphiumids, and ambystomatids). *Siren* has greatly simplified epaxial myomeres, rivaled only by those of the newts and proteids. In *Siren* a slight tertiary complexity has been added to a secondary simplification, owing to the constraints of anguilliform locomotion. The structure of the hypaxial and epaxial musculature suggests strongly that sirenids were derived from opisthocoelous ancestors. Although Auffenberg (1959, p. 264) claims that "*Amphiuma* can more easily be derived from the primitive [sic] condition in *Necturus* than can . . . *Siren*," the reverse is in fact true.

Hypaxial musculature (see Fig. 87).- Except for Maurer (1892), the *subvertebralis* of this genus has never been described. The *subvertebralis* is highly derived and quite different from that seen in the salamanders described above, but the basic pattern is quite similar to that of newts (especially *Notophthalmus*). The structure of the *subvertebralis* in *Siren* can only be derived from an ancestor that was fully opisthocoelous and lacked posterior flexures.

A large lamellar plate (the second alar process, see Fig. 1E) projects anteriorly from the transverse process. Each plate extends forward of the anterior cotyle, forming a projection on each side of the centrum. This structure is approached by *Notophthalmus*, which lacks the anterior projection, however. A thick muscle arises from each anterior projection and from the anterolateral edge of each second alar process. This muscle fans anteriorly to originate on the ventral surface of the second and first alars and lateral edge of the centrum of the next anterior vertebra. A long, thin septum attaches to the forward projection from the second alar. This extends anteromedially into the muscle block just described.

This "basapophyseal" muscle is not homologous with the anterior basapophyseal muscle described in ambystomatoids and cryptobranchoids. Auffenberg (1959, p. 264) states that "the deeper portions of the subvertebralis complex is [sic] basically similar in all three genera [*Necturus*, *Siren*, and *Amphiuma*], except for the strong basapophyseal attachments in *Amphiuma*." This observation is incorrect: as shown in Figures 30, 45, and 87, the *subvertebralis* is fundamentally and markedly different amongst the three genera, with *Siren* being the most derived.

Dorsal to the "basapophyseal" muscle is a layer of subvertebral musculature extending anterolaterally between the transverse processes. This layer is continuous with the *o. internus* laterally and ventrally. Next to the vertebrae the fibers run anteroposteriorly. This unit is very simple and strongly resembles that of certain newts.

The spinal nerves exit intravertebrally through a small foramen in the wall of each neural arch just below the interzygapophyseal crest. From this point the nerves extend through the *subvertebralis* and then posteroventrally between the *transversus* and *o. internus*. Along the lateral body wall, each nerve passes along the posterior edge of a myocomma.

Lateral abdominal musculature (see Figs. 87, 88, and 89).- This unit is extremely thick, but composed of the expected divisions in their usual positions. The *o. e. superficialis* is thin, with the muscle fibers proceeding posteroventrally between the segmenting myocommata. Dorsally the *o. e. superficialis* slightly overlaps the expaxial musculature and extends ventrally for only a short distance, exposing much of the *o. e. profundus*. Ventral to the horizontal septum and deep to the *o. e. superficialis* is found a relatively thin band of anteroposteriorly aligned muscle fibers, the *rectus lateralis*.

Next internally is the *o. e. profundus*, a thick muscle with its fibers extending posteroventrally between the myocommata. Ventrally the *o. e. profundus* blends completely with the *rectus abdominis*. Deep to the *o. e. profundus* is the *o. internus*, the fibers of which are a ventral continuation of the *subvertebralis*. Fibral orientation is anteroventral, more or less at right angles to the fibers of the *o. e. profundus*. Ventrally the *o. internus* blends with the *o. e. profundus* to form the *rectus abdominis*.

The deepest layer of the lateral abdominal musculature, next to the peritoneal cavity, is the *transversus*. This is not divided by myocommata, but externally (next to the *o. internus*) the myocommata partially invade the *transversus*. The *transversus* is very thick, with fibers extending dorsoventrally. Dorsally it is directly connected to the vertebral column by tough fascia, which attaches along the anterolateral edge of the second alar, the posterolateral edge of the first alar, and to the lateral edge of the posterior cotyle. This situation is derivable from that of the newts (especially *Paramesotriton*).

The *rectus abdominis* is not a distinct unit, but is formed from the merging of the *o. internus* and *o. e. profundus*. Medially the *rectus abdominis* forms a cone-in-cone arrangement, with adjacent myomeres extending anteriorly into their neighbours. Owing to this arrangement, a transverse section through the trunk shows a complex pattern of muscle blocks in the area of this unit. Thus, in section, it appears as though there is a distinct and complex *rectus abdominis*, although it is in fact simple.

If the lateral abdominal musculature is spread laterally and the *transversus* removed, the pattern of the myocommata and myomeres becomes clear. From each transverse process the myocomma proceeds posterolaterally. At a point near the ventral terminus of the *transversus* the myocomma begins to arch gently anteriorly, so that it comes to extend anteromedially to the centre of the *rectus abdominis*. The myocommata incline posteromedially through the *o. e. superficialis*, *o. e. profundus*, *o. internus*, and barely into the *transversus*.

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Chapter III

PRINCIPLES OF SYSTEMATICS

A. Morphology and Phylogeny

i) Phylogenetic reconstruction

Various attempts, both explicit and implicit, have been made to define principles of phylogenetic reconstruction. At one time, characters having little or no adaptive significance were believed to be especially useful in phylogenetic study. Writing of the Amphibia, Noble (1931, p. 90) concluded with respect to patterns of "dentition, pupil form, pectoral girdle, [and] tongue form," that "many of these parallel changes have no known functional significance." As he used these as important diagnostic features, it seems these "characters of Amphibia [that] have no functional significance" (Noble 1931, p. 93) were considered good taxonomic characters. Darwin (1859), however, recognized long before that, by and large, the most important taxonomic characters are of significant "physiological" (= functional) import (see also Cain 1959b). The characters used by Noble in his classifications are certainly important, but precisely because they are functionally crucial.

Numericists would argue that there should be no selection or weighting of characters (see Sneath and Sokal 1973), but that all (or as many as practicable) features of organisms should be used in the determination of relationships. As noted below (also Hull 1970), this philosophy is both impossible to implement and undesirable as an ideal.

Some characters prove more significant (and more useful) than others in reconstructing phylogeny and in the production of a classification. Nevertheless, in less extreme form, the claim that reconstruction of phylogeny should be based on many characters is true.

Cladistic systematists insist on using only shared-derived (or apomorphic, see Hennig 1966) characters. For example, although not explicitly cladists, Wake and Özeti (1969, pp. 124-125) state that "information concerning relationship in primary groups (e.g., the family Salamandridae) is contained only in derived character states. Resemblance that results from characters shared in states that are primitive for the primary group has no phylogenetic information." In a restricted sense this claim is true (and recognized well before the advent of cladism). However, it is not true to claim that characters presumed to be primitive hold no phylogenetic information. What such characters lack is cladistic information, the confusion resulting from usage of phylogenetic as an improper synonym for cladistic. Phylogeny includes two different, but linked, components: cladistic and patristic. Perhaps to emphasize the distinction, rather than writing of "phylogenetically" (read cladistically) significant characters, one should use characters of evolutionary significance. Evolution subsumes phylogeny, which subsumes cladistic relationships, but not vice versa. Common retention of presumed primitive features indicates similar evolutionary history, owing to conformity of genotype and selective regimes. All characters, whether interpreted as relatively primitive (plesiomorphic) or relatively derived (apomorphic), hold a certain amount of evolutionary, and hence phylogenetic, information.

The argument against exclusive use of presumed apomorphic features becomes stronger upon rejection of cladistic assumpsions and acceptance of the concept of the morphocline (see Maslin 1952, and below). That is, rejecting the (subjective) assertion that only cladistic relationships should be of interest, one necessarily rejects the claim that primitive characters are valueless. Reaching this point, it is necessary to consider principles of phylogenetic reconstruction.

Hennig (1966) discussed the criteria to be used in the determination of the polarity of a transformation series (or morphocline), suggesting the following:

1. Geological character precedence (biostratigraphic criteria).
2. Chorological progression: advanced characters tend to be found in those species that have departed furthest geographically and/or ecologically from the initial ancestor.
3. Ontogenetic precedence (ontogeny recapitulates phylogeny).
4. Correlation of series of transformations.

In addition, Hennig (1966) explicitly recognized that reversals, convergence, and parallelism would cause difficulties in utilization of these criteria. His suggestions are, by and large, valid, but are sometimes ignored by some who claim to be his followers.

I suggest the following as criteria to be used in the determination of morphocline polarity, and thus of phylogeny:

1. That character state found in the earlier fossil representatives of a higher taxon should tend to be the more primitive. This is based on the theory of evolution by natural selection as applied to the sampling of true phylogeny by the fossil record. It is (or should be)

obvious that an actual evolutionary sequence must have the ancestral characters occurring prior to the more derived. Earlier fossil species, therefore, tend to approximate more closely to the ancestral state and are judged to be primitive. As recognized by Hennig (1966), paleontology often provides clues as to actual ancestral states. Only paleontological data are truly historical, allowing one to infer actual time dimensions (Simpson 1961).

One of the more powerful arguments for the inclusion of biostratigraphic data in the determination of ancestor-descendant and sister-group relationships is that, in geology, the concepts work. Dating and correlation of fossiliferous rock sequences have been exhaustively tested throughout investigations since the time of William Smith (see Wood et al. 1941, on correlation of the North American Tertiary by means of fossil mammals). The system has been critically used and not falsified. In addition, as noted, the fact of descent with modification stands in powerful support of the use of biostratigraphic data in phylogenetic investigations (for a contrary view, see Schaeffer et al. 1972).

Geological criteria are most important in groups possessed of an adequate fossil record (e.g., early reptiles and amphibians, see Romer 1966 and references therein; horses, see Simpson 1951) and it is evident that urodeles lack an adequate record. The known fossil species belong to several different families, and are scattered temporally and geographically. Owing to this sporadic record, it is not possible to place similar specimens in any sort of morphological sequence (perhaps excepting the Batrachosauroididae, see below).

It is also evident that the more derived, neotenic species have been disproportionately sampled in the Mesozoic and early Cenozoic. The fossil record may be used to the extent of documentation of first known occurrences so as to aid inferences about minimum times and areas of origin. Nevertheless, in study of the interfamilial relationships within the Caudata the living species must form the basis for a system into which the fossil taxa may be fitted. Although with salamanders this is the only possible approach, it is not to be taken as advocating a devaluation of the fossil record.

2. That character state found in a higher taxon that is, on independent evidence, determined to be relatively plesiomorphic should tend to be primitive. This is Hennig's (1966) correlation of transformation series, and basically derives from Cuvier's "Law" of the Correlation of parts. The entire organism is the unit of selection (Mayr 1963), each structural unit or complex being acted on in the context of relationship to and interaction with other such units within the animal. As noted by Cuvier, for example, ungulates tend to have high-crowned, grinding teeth and hoofs, in addition to other correlated features. In spite of the celebrated exception of chalicotheres, the "law" is true as an observational generalization. While recognizing mosaic evolution to be a very real phenomenon, this criterion can be used as an aid in the elucidation of morphocline polarity.

3. A character state shared by members of one taxon with members of a related taxon will tend to be primitive (for at least one of the taxa), especially when the character state is located at the ends of

the two morphoclines. This is the principle of ex-group comparison. For the Caudata, comparison with anurans, caecilians, and fossil amphibians may indicate the relative primitiveness of certain character states. For example, anurans generally have external fertilization, as do two of the living families of urodeles. This feature is also shared with "lower" vertebrates (fish), and is likely to be primitive for the Caudata. In the same way it may be said that paired premaxillae with short nasal spines are probably the ancestral state, retained in hynobiids and cryptobranchids.

The criterion may also be used within the Caudata: for example, the structure of the trunk musculature and vertebrae in the Ambystomatidae. Based on correlations of transformation series, general structure, and ontogenetic evidence, the trunk musculature and vertebrae of hynobiids are probably the most primitive of living salamanders. This accepted, the close resemblances of *Ambystoma macrodactylum*, *A. maculatum*, and their allies to hynobiids in this character complex, and the divergent, foetal condition of *A. tigrinum* and its allies cast serious doubt on Tihen's (1958) determinations of the primitive vertebral state for ambystomatids (see below). The same argument applies to the frontosquamosal arch, which is almost certainly derived within the Salamandridae.

4. Data from studies of different ontogenetic states. Developmental stages from larva through to metamorphosed adult can provide valuable information for use in phylogenetic investigations. This is especially true of salamanders, which have utilized paedomorphosis (evolution via neoteny and paedogenesis) to a large degree. The Caudata are excellent examples of the concepts of de Beer (1958) and of the

rejection of "recapitulation" as a general law. Features that appear primitive on first view are often shown to be derived owing to paedomorphosis. In the Caudata, the simple is often the apomorphic, in spite of what intuition might indicate, as is shown by the structure of the skull and trunk musculature. On the other hand, it has been assumed that complex lateral abdominal musculature is the more primitive (e.g., Noble 1931). Nevertheless, it is more likely, upon considerations of larval patterns, that the possession of many layers of abdominal musculature is a derived, foetal condition. Ontogenetic evidence was also used by Wake (1966) in his elucidation of the primitive and derived states of the premaxilla in plethodontids, and has been necessary in the proper interpretation of the family Ambystomatidae (see below).

It is to be emphasized that none of these criteria are infallible. All possible data must be considered in order to arrive at reasonable conclusions. Maslin's (1952) suggested criteria can also, depending on circumstances, be used as clues in phylogenetic reconstruction, but caution is necessary. He (1952, p. 69) assumed that "morphoclines are partially or entirely identical to the chronoclines from which they are derived." Although this could well be true in any given case, it might just as easily be false. I know of no empirical or reasonable theoretical considerations that would tend to support this as a valid generalization. Each population travels a unique evolutionary path, changing as directed by selection so as to maintain adaptation. There is no known mechanism that might cause primitive organisms to remain so, unless this is adaptive (see Brundin 1972a for a different, although vitalistic, view).

Maslin (p. 56) also believed that "convergence is relatively rare." Study of the fossil record (e.g., early bony fishes, early reptiles, and mammal-like reptiles) and of living populations (e.g., the *subvertebralis* of newts and certain plethodontines) documents the weakness of this assumption. A tremendous amount of parallelism and convergence has been recognized and much must go unseen. Hennig (1966) noted that these phenomena must be carefully considered in phylogenetic research.

To work, Maslin's criteria and those suggested above must be augmented with detailed studies of the transformations within the morphoclines. That is, functional relationships and environmental correlations (see Cain 1959b) must, in so far as possible, be studied and the most probable sequences determined. Moreschalchi (1973) notes the necessity of deciding what known structures could have served as ancestral states. In this way, ancestral states may be inferred from features believed to be primitive.

In spite of such cautions, I suggest that Maslin's criteria are basically reasonable and useful. The main criticism is, perhaps, of the possibility that strict utilization of them would make phylogenetic analysis rigid. Nature is multiform and complex, making it necessary that operating principles be broad and flexible, with the organisms rather than the rules providing the ultimate guide. Principles are generalizations and not necessarily completely true; one must be ready to discard them whenever they are contradicted by nature.

I take the position that "good" phylogenetic characters have the following features:

1. They are part of a coherent adaptive complex, the functional significance of which is more or less understood.

2. They can be studied in a series of lower taxa and the differences and functional reasons for the differences can be studied by means of morphoclinal analysis.

3. They are useful for ex-group as well as in-group comparisons.

4. They are preservable in fossil specimens, so as to allow direct comparison of past and present.

Darwin (1859) discussed "good" characters in classification, a treatment that still has importance today. He (1859, p. 415) stated that "almost all naturalists lay the greatest stress [in classifying] on resemblances in organs of high vital or physiological [i.e., functional] importance," but "the mere physiological importance of an organ does not determine its classificatory value." Darwin (p. 417) noted that "a classification founded on any single character, however important that may be, has always failed; for no part of the organism is universally constant." The usefulness "of trifling characters, mainly depends on their being correlated with several other characters of more or less importance" (Darwin 1859, p. 417). In these quotations, substitution of "phylogenetic reconstruction" for "classification" shows the importance of Darwin's ideas to present-day phylogenetic analysis.

In many cases the adaptational significance of a given character is obscure or unknown, and this has been a problem in the present study.

Nevertheless, when differences in character states can be related to changes in adaptive strategies and environment, it is easier to interpret morphoclines. If this approach is taken, the phylogenetic information in the characters increases and phylogenetic reconstruction becomes more meaningful (Cain 1959b). Upon acceptance of the fact that structures usually exist for precise functional reasons, this is the only logical approach.

Functionally important character complexes have been, in practice, accorded heavy weight in phylogenetic studies (Darwin 1859). Feeding and locomotory systems are important in the study of the relationships of fishes (Greenwood et al. 1973), and have been among the more extensively used in the systematics of salamanders (Noble 1931, Regal 1966, Wake and Özeti 1969). Such systems are clearly important to the continued survival of lineages, and it is often possible to determine functional reasons for the differences between taxa. This allows characters to be weighted more validly.

In investigating the interfamilial relationships of the Caudata (or in any other such study), it is necessary to consider each family in detail. It is not sufficient to choose one or two representatives from each family and then hope to develop realistic hypotheses of relationship between families. First, intrafamilial morphoclines must be clearly known. Once morphocline polarities within families are decided, comparisons can be made between families. In my study, the new data come mainly from the trunk musculature and vertebrae. As many genera as possible from each family were dissected, allowing for comparison of vertebral structure and correlated patterns of the myomeres within families. Each familial morphocline may then be compared with those of other families in order to match end points and determine polarities. In some cases (e.g., sirenids and amphiumids) familial "morphoclines" necessarily consist of a single character state. Once interpreted, the morphoclines allow theoretical judgements as to probable phylogenetic sequences.

Utilization of the morphocline allows flexibility and extensive use of in-group and ex-group comparisons. Judgements can be made as to what state could, in theory, most readily have given rise to other states, both within and between families. Furthermore, the congruence, or lack thereof, between morphoclines of different characters is more apparent. The flexibility of this approach should be regarded as a virtue, but perhaps its lack of rigidity deprives it of the qualities of a panacea, contributing to its lack of use.

It is essential that characters be useful for ex-group comparisons. Characters having only one state within a family and that are not derivable from a particular state in another family have little value in the determination of either intra- or interfamilial relationships. It is necessary that characters vary from taxon to taxon and that, if possible, they also vary within taxa. For example, as the nasolabial groove is unique to the Plethodontidae, derivable from no known structural ancestor, and does not vary significantly within the family, it is quite useless as a character on which to base any phylogenetic theory. This was overlooked in Edwards' (1976) phylogenetic treatment of the Caudata, in which the nasolabial groove is purported to have some (unstated) sort of significance.

A more definite example from the Caudata may be illustrative. The *subvertebralis* shows marked structural diversity within this order, with most of the families having a more or less unique and readily distinguishable configuration of the myomeres. In addition, the Ambystomatidae, Plethodontidae, and Salamandridae each show an intrafamilial morphocline of this unit and, together, a single interfamilial cline (see Fig. 90 and above descriptions). In ambystomatids the morphocline may be considered to show only a single state, although this is an oversimplification. As indicated by comparison with the Hynobiidae, ambystomatids have the primitive (phenetically and probably ancestrally) sort of well-developed anterior basapophyseal muscles and associated flexures. Plethodontids display a distinct morphocline running from the primitive condition in *Plethodon*, with the posterior flexures shifted medially and the anterior basapophyseal muscles suppressed; through *Eurycea*, with distinct development of neomorphic posterior basapophyseal muscles; to *Pseudotriton* and the desmognathines, with progressive increase of the posterior basapophyseal muscles. In addition, a secondary morphocline includes species of *Plethodon*, *Batrachoseps*, and certain bolitoglossines: all trace of the subvertebral flexures is lost, converging upon the salamandrid newts. In the Salamandridae there is a single, simple morphocline including *Salamandra* at the more primitive end retaining posterior flexures and the newts, with loss of these flexures.

Accepting that the *subvertebralis* of hynobiids and ambystomatids exhibits the primitive condition, it is possible to compare and interpret the morphoclines. The basic trend is from complex to simple, a common situation in the Caudata. The plethodontid morphocline may be joined to that of the ambystomatids, with *Plethodon* representing the more primitive end of the cline. Similarly, the salamandrid cline joins to the plethodontid, with *Salamandra* exhibiting the primitive structure. The resulting scheme to some extent mirrors what I understand to be the phylogenetic history of the three families, but it is to be stressed that this joining of familial morphoclines of a single structural complex does not produce a phylogeny, although it is a reflection of it. Evidence from other systems must also be considered and structural complexes that are functionally linked with the *subvertebralis* must be interpreted, such as the nature of the intercentral joint, epaxial myomeres, lateral abdominal musculature, and the general configuration of the vertebrae. When the different morphoclines have been analyzed and compared, contradictions may be resolved, judgements made, and hypotheses of relationship proposed.

Finally, in consideration of morphoclines it must be remembered that ancestors existed in the past. At best, contemporaneous species can only provide structural approximations to true ancestral states. Whereas it is perfectly acceptable to derive plethodontids from an ambystomatid-like ancestor, which (if known) would be properly classified in the Ambystomatidae, it is not meaningful to derive living plethodontids from living ambystomatids. By contrast, in the case of plethodontids and salamandrids, data from other systems (e.g., vomerine teeth, lunglessness, and structure of the middle ear) tend to contradict the derivation of the latter from a plethodontid ancestor. Rather, descent of the two families from a common ancestor (probably most similar overall to plethodontids) seems the most reasonable interpretation.

Owing to the historical nature of phylogeny, it is helpful if characters used in studying living organisms be applicable to fossil specimens, so that past and present are more directly comparable. With respect to salamanders, trunk musculature provides such a complex of characters. In many cases, the sort of trunk musculature is directly reflected in the structure of the trunk vertebrae. Thus, fossil vertebrae having posterior or anterior basapophyses (for example) are readily interpretable in terms of extant salamanders (see below). Similarly, cranial osteology, spinal nerve exits, and ossified hyobranchial elements can often be used in both fossil and Recent taxa. By contrast, phylogenetic reconstructions based exclusively on patterns of courtship, karyology, or structure of the ear are not useful with respect to fossil specimens.

ii) Karyology

Study of the number and structure of chromosomes and of the amounts of nuclear DNA in different species provides information potentially of use in phylogenetic study (see Chiarelli and Capanna 1973, Moreschalchi 1970, 1973, 1975). However, the relative importance of karyological evidence as opposed to data from other aspects of the phenotype is not clear. As karyological data have been used as important components in phylogenetic reconstructions of the Caudata, it is necessary that they be considered. The karyotype is an important aspect of the phenotype, but must be studied and interpreted in the same way as any other feature (see also Moreschalchi 1973).

One must be cautious about any single character used to construct a phylogeny (Darwin 1859). It has been argued that karyotypes have "a lower adaptive value as compared to other morphological features . . . [and] for this reason, karyotype [sic] variations reflect general phyletic lines" (Benazzi 1973, p. 5). The adaptive nature of the karyotype may be debated, but it is probable that this part of the phenotype is constructed in just as adaptive a fashion as any other (Cain 1964, Nikolsky 1976). Enthusiasm for karyology is another attempt to use little understood (or "non-adaptive") features as important taxonomic characters, even though such usage is not valid (see Darwin 1859, pp. 414-417, Cain 1964).

Environmental correlations in the context of the theory of natural selection can provide suggestive, although tentative, evidence of adaptation for any character. For example, large amounts of DNA and large cells in dipnoans and paedogenic salamanders correlate with freshwater environments subject to changes in temperature, salt concentrations, and ionic balances. Metabolism is slow in relation to necessary adjustments to environmental flux (see Szarski 1970, 1976). These correlations indicate the probable presence of adaptation. Goin et al. (1968) noted a correlation between smaller amounts of DNA in amphibians and more rapid progress through larval stages. Papers by Olmo (1973), Olmo and Morescalchi (1975), and Morescalchi (1973, 1975) contain information on the adaptive nature of the amphibian karyotype. Nikolsky (1976) provides a more general model to account for variations in chromosomal number in fish.

Morescalchi (1973, p. 238) noted that "the cytotaxonomic study of the higher families [of amphibians] is found to be immediately useful only at very general levels." However, "the integration of these [karyological] data with anatomical or other types of data . . . may always prove useful indications for a precise definition of the evolutional [sic] lines followed by these vertebrates." The same may be said for any structural feature. In order to determine the primitive chromosomal situation in the Amphibia, Morescalchi (1973) used two criteria:

1. A model common to the more "generalized" forms of the three orders.
2. A karyotype that could have given rise to a second, but from which it could not be as readily derived.

These lead to the same model: a karyotype with a high number of chromosomes, many acrocentric chromosomes, and many microchromosomes. Morescalchi (1973) interprets the Cryptobranchoidea as primitive, with asymmetrical, bimodal chromosomes; those families with asymmetrical, unimodal chromosomes as intermediate (Sirenidae and Proteidae); and those with symmetrical chromosomes as most derived (Amphiumidae, Ambystomatidae, Plethodontidae, and Salamandridae). Except for the position of sirenids and proteids, which I believe to be owing to secondary reversion (see below), Morescalchi's reconstruction (1973, fig. 14) is quite similar to mine.

Karyology can contribute to evolutionary studies, but such evidence must be treated cautiously. There does seem to have been an overall trend to reduce chromosomal number within the Caudata, but the reasons for this are unknown and it does not appear to have been universal. The sirenids are perhaps tetraploid (Morescalchi 1975, Morescalchi and Olmo 1974). Cryptobranchids are all but certainly derived with respect to hynobiids, yet the living species of *Cryptobranchus* have higher numbers of chromosomes than do hynobiids. In the structure of the trunk, proteids are derivable only from an opisthocoelous ancestor. In spite of a relatively high chromosomal number (2n=38), they cannot be directly derived from hynobiids. In such cases gross anatomy takes precedence over karyology.

In more or less paedogenic, permanently aquatic salamanders (Amphiumidae, Proteidae, Sirenidae, and Cryptobranchidae) there has been an increase in the amount of cellular DNA (Morescalchi 1975, table II). This gain can only be interpreted as convergent in these groups and appears to be of a purely adaptive nature (compare dipnoans). In spite of the apparent lack of overall close correlation between phylogeny and karyotype throughout the Caudata, there are correlations on lower levels. Karyology certainly provides clues to phylogenetic understanding, but it is surely more profitable to investigate adaptation than to "reconstruct" questionable or nontestable phylogenies based on single (even though ill-understood) characters.

iii) Concepts and Cautions

Comparative anatomy and homology.- Zangerl (1948) advocated a clear separation in morphology of factual results (gained from observation and comparison) from the interpretation of these results. His criticism of the trend towards not publishing the data (descriptions and comparisons) in favour of reporting only the interpretations is well taken. Theories hopefully conform to observations, and to report only the former is not scientific. In this regard, an historical perspective is helpful: the timeless works are those filled with good factual observations. As science evolves, theories may change, but the descriptions and observations remain useful. The most revolutionary and influential contribution to biology, *On the Origin* (Darwin 1859), owed its original (and hopefully continuing) theoretical impact to the detailed facts marshalled to support the theory of evolution by natural selection.

In spite of this agreement, acceptance of Zangerl's (1948) argument for a divorce of data collection from interpretation is not possible. As noted by Darwin (1859), data collection cannot possibly take place in the absence of theory. "I can have no doubt that speculative men, with a curb on, make for the best observers" (C. Darwin, in Darwin and Seward 1903, II, p. 133). It is neither possible nor profitable to attempt observations untouched by theory and then, subsequently, decide what they might mean. The problems with Baconian research have been discussed by Hull (1970, 1974) and Ghiselin (1969), among others.

Zangerl (1948, p. 354) states that "morphological concepts are factual generalizations from observed structural relationships and as such *they do not and cannot carry phylogenetic implications*" (italics original). He argues that phylogenetic inquiry lies outside the area of morphology, which is not to be harmed by theorizing. Given the present evolutionary framework of biology, I do not believe that this position is tenable. Rather, morphological concepts of necessity carry phylogenetic implications. In studies such as mine, morphology serves as a tool to elucidate the relationships of the families of urodeles, among other things. Theory and observation must, therefore, proceed hand in hand in a relationship of reciprocal illumination (Hennig 1966).

Even in "pure" comparative anatomy concepts are important. Those features that are compared must be homologous in the evolutionary or phylogenetic sense. Given that evolution (descent with modification) has occurred, we *define* homology as based on derivation from common ancestry. Homology is a definition, not a theory. Whether two structures are homologous is another question. Structures are homologous if one hypothesizes that they have been derived from a feature possessed by an ancestor common to the taxa being compared. Phylogenetic conclusions are drawn by observing and comparing structures in different taxa to decide whether they are homologous. A conclusion that structures are homologous is also a conclusion as to the genealogical relationships of the organisms possessing the structures, but this is not circular. The definition of homology may be circular, but as definitions are tautological such a comment is not profound. The critical question is whether the application of the concept of homology is circular. This, of course, does not have to be the case.

Primitiveness.- The concepts of phenetic and ancestral primitiveness are important in phylogenetic analysis, and the two are not necessarily synonymous. Phenetic primitiveness is used, for example, in groups of contemporaneous organisms when it is stated that taxon (or character) A is plesiomorphic with respect to taxon (or character) B. This means that, given present information, one taxon can in principle be derived from the structural conditions of another. In phylogenetic study it is hoped that phenetic primitiveness approximates to ancestral primitiveness and that structural ancestors reflect real ancestors. However, whether or not taxon (or character) A is truly ancestral is another matter. Ancestral primitiveness is used when it is stated that taxon A *is* ancestral to taxon B. In such cases the fossil record is, of necessity, involved because the taxon hypothesized to be ancestral must have preceded the descendant.

As soon as a lineage splits, or when one gives rise to a second, the two lineages are subject to continuous selection in the context of differing genotypes and environments. There is, therefore, no reason to argue that a plesiomorphic taxon necessarily preserves partially or entirely the structural conditions of the true ancestor. Such may be so, but that is to be determined on the merits of the individual case and with the deciding criteria coming, if possible, from the fossil record.

Parsimony.- The concept of parsimony is often used in science and is frequently resorted to when two opposing theories are compared. It is held that, in absence of other information to be used in testing, the choice between two otherwise equally plausible hypotheses is to be made on the basis of the principle of parsimony. An hypothesis is to be constructed with a minimum number of supporting assumptions, the reason being that simpler hypotheses are more readily testable. With fewer supporting theories (assumptions) it is easier to test the major theory itself. Otherwise, any test or observation that might seem to falsify a theory could be owing simply to the invalidity of one or more of the supporting assumptions, rather than to problems with the major theory. Parsimony does not derive from the assumption that nature is simple, but from the methodology of science (see Popper 1968a,b).

Parsimony may be misused in support of special interests. For example, it should not be claimed that the more parsimonious phylogenetic reconstruction is necessarily the one with the fewest number of branching points. "The fact that one bases a method of phylogenetic interpretation on parsimony does not require that evolution be a parsimonious process, although many researchers believe it is" (Hecht and Edwards 1976, p. 672). Simple cladograms may well be, at base, extremely unparisimonious. That is, the assumptions necessary to support a simple (or simplistic) phylogenetic reconstruction may well be numerous. A simple phylogeny with numerous assumptions would then be less parsimonious than a phylogenetic reconstruction with more branching points but fewer supporting assumptions.

Embryology.- Although data from ontogeny can be extremely useful, especially with salamanders, the biogenetic "law" of Haeckel is here explicitly rejected. In spite of attempted restoration, the concept has been so effectively negated (de Beer 1958, Ewer 1960) as to need little discussion. Ontogenetic information is as important as that from any other area, but it is no more important and cannot be used to substitute for good fossil evidence. The use of recapitulation necessitates adherence to evolution by means of gerontomorphosis, that is, of phylogenetically new adult stages being added (see de Beer

1958, pp. 36-37). As documented by de Beer (1958) and almost ideally confirmed by salamanders, however, paedomorphosis (evolution by accentuation of larval stages) has been a much more common occurrence. Furthermore, when the embryo is properly viewed as an adapted system providing for the most efficient production of the adult stage, the "law" that ontogeny recapitulates phylogeny is clearly false.

Numerical analysis.- As a general rule, it may be said that the problem in phylogenetic research is not inability to handle large amounts of information, but an inability to order the data theoretically and reasonably. Numerical methods are often invaluable tools, but they cannot substitute for theoretical and interpretive input (see Hull 1970, Ghiselin 1969, p. 21). Characters are to be chosen for informational content and applicability (see above), not because they are simply available and readily measured and coded.

In attempts to develop more "rigorous" classifications and phylogenetic reconstructions, workers have turned to cluster analysis of many characters. Krogh and Tanner (1972) argue for the extensive use of computer techniques in systematic work, but their study of the Ambystomatidae suffers from problems that computer analysis cannot remove. As they point out, the hyobranchium and its associated musculature provides all of their characters. Therefore, although 48 factors were used in analysis (Krogh and Tanner 1972, pp. 59-61), the outcome is still a single character phylogeny. The hyobranchium is an integrated, although complex, system composed of intricately related structures (see Larsen and Guthrie 1975, Lombard and Wake 1976, 1977). Treating such a system as a large number of component parts ("characters"), although useful for functional analysis, is more likely to be misleading than enlightening in a phylogenetic study. Further, although a valuable contribution to comparative anatomy, the work of Krogh and Tanner (1972) suffers from lack of theoretical interpretation. Before cluster analysis can be used to elucidate phylogeny, characters must be weighted by judgements as to presumed primitive and derived states, structural sequences, and functional *raisons d'être*.

In their study of intergeneric relationships within the Salamandridae, Wake and Özeti (1969) made interpretations of primitive and derived states, thus partially analyzing the data prior to cluster analysis, and used characters from more than one adaptive complex. Characters judged as primitive were rejected as having no phylogenetic information, however, and owing to misinterpretation in several cases (see below) and the misuse of correlations of character states, analysis was partially biased. Character states for which judgement as to primitiveness was not possible were assumed to be primitive (or derived) if they happened to correlate with another character believed to be primitive (or derived). Owing to misinterpretation of the nature of the frontosquamosal arch (see below), several linked misidentifications followed. Finally, the phenomenon of convergence was ignored in the case of *Salamandrina* (probably owing to over-utilization of characters from the hyobranchium), and ex-group comparisons with other families, which are essential in determination of morphocline polarity, were not possible owing to lack of information. These criticisms do not devalue the contribution of Wake and Özeti (1969), whose descriptions are important, but show the need for caution in numerical analysis of data.

Edwards' phylogenetic reconstruction.- Finally in this section on cautions, the most recent phylogenetic analysis of the Caudata must be considered. Edwards (1976) proposed a new classification and phylogeny of salamanders. The study purports to be based on several characters, but the phylogenetic information present in many of these is low or nonexistent. His phylogeny and the classification that follows from it are ultimately double character systems, based on chromosomal number and the pattern of spinal nerve exits. These two characters are certainly important (and his proposals are close to mine), but other data are ignored.

Edwards (1976, pp. 318-321) uses the following characters:

1. *Presence or absence of the angular bone.* This serves only to distinguish the Cryptobranchoidea.

2. *Internal or external fertilization.* Again this serves only to distinguish cryptobranchoids (and questionably sirenids) from other salamanders. The information provided by Salthe (1967) is not utilized.

3. *Patterns of replacement of vomerine teeth.* These patterns are not compared across familial lines (see Regal 1966) and there is no analysis of morphoclines.

4. *Chromosomal number.* This is useful for interfamilial interpretations.

5. *Pattern of exits of spinal nerves.* This is also useful across interfamilial lines.

6. *Number of gill slits.* This feature tells little or nothing of phylogenetic relationships of the families, the numbers are not compared across familial lines, and there is no interpretation provided (see also Hecht and Edwards 1976).

7. *Presence or absence of the second epibranchial in the adult.* This is a loss character (see Hecht and Edwards 1976) serving only to distinguish cryptobranchoids and, perhaps, sirenids.

8. *Free or fused columella.* The treatment of this character is oversimplified. There is in fact a wealth of phylogenetic information contained in the auditory apparatus (Kingsbury and Reed 1909, Reed 1920, Monath 1965), which is ignored in this study, leading to misleading results.

9. *Presence or absence of the lacrimal bone.* "The complete loss of a character state does not indicate evolutionary direction or relationship, nor does it indicate whether the distribution among taxa is the result of parallel or convergent evolution. It is impossible to determine whether the loss of the character occurred independently or was the result of directional selection. All relationships based on loss of shared and derived characters have zero state information and must be seriously questioned" (Hecht and Edwards 1976, p. 655).

10. *Presence or absence of the ypsiloid cartilage.* This feature is not useful in interfamilial interpretation of salamanders as there has been demonstrable independent loss in various lineages (see also Hecht and Edwards 1976, p. 655).

11. *Presence or absence of maxillary bone.* This is another character having no informational content for interfamilial relationships. It is a loss character and also correlates with paedomorphosis (see also Hecht and Edwards 1976).

12. *Presence of the nasolabial groove.* This feature has no informational content at the interfamilial level, as it is unique to

plethodontids and lacks structural antecedents in other families. "The apomorphous features characteristic for a particular monophyletic group (present only in it) can be ignored in discussing its relationships to other groups" (Hennig 1966, p. 90).

There is a tendency for all workers to make sole, or major, use of certain characters (either those with which one is working or that tend to support a certain theory) in phylogenetic analysis and to ignore or explicitly reject others. Characters or morphoclines that tend to controvert one's phylogenetic models must be discussed, however, and it is necessary to explain why contradicting facts are considered to be of less importance than the supporting evidence. In their recent consideration of the relationships of the Proteidae, Hecht and Edwards (1976) discuss 18 characters used by previous workers to demonstrate monophyly for the family. Their detailed treatment of evidence in conflict with their hypothesis of polyphyly is admirable, allowing one to readily see areas of disagreement and to clearly follow the arguments. In this sense, my disagreement with their conclusions (see below) is incidental.

As recognized by Darwin (1859), divergence and extinction are real phenomena, creating the gaps observed between living taxa. This being so, reconstruction of phylogeny of Recent animals in the absence of paleontological data is especially difficult, unless clear and reasonable principles are used. These criteria must be consistent with evolutionary theory and with information from organisms that have a good fossil record (i.e., mammals). Principles derived from organisms lacking such a record (that is, for which information as to what really happened is absent) are necessarily likely to be less realistic, especially when they conflict with information from phylogenies that are reasonably certain. The caudate amphibians present the situation, seen also in fish and insects, of abundant living representatives and a poor fossil record. There is, as yet, no possibility of utilizing the fossil record to test the conclusions reached by previous workers and in this study. Therefore, my work must be tested on its own merits as to whether it is parsimonious, internally consistent, and in agreement with presently known data. The suggested relationships are testable hypotheses (or predictions) as to what should be expected in future studies if they are true. Hopefully those studies will include paleontological research.

B. Biological Classification

i) Introduction

Competent biologists accept that the concept of evolution best explains our observations of the organic world. Darwinism is therefore the theoretical basis of biological inquiry, including the discipline of taxonomy. This being so, biological classification should reflect our understanding of the evolutionary history of organisms. It is probable that, perhaps excepting some pheneticists, all systematists would agree with this thesis, but how best to express evolutionary relationship remains an area of contention.

As in politics, taxonomic theorists are divided into three camps — pheneticists (Sneath and Sokal 1973), evolutionists (Darwin 1859, Mayr 1969, 1974, Simpson 1945, 1961), and cladists (Brundin 1966, 1972a, Hennig 1966). Unfortunately, the debate has also become political, with emotion substituting for reason and dogma for argument. Nevertheless, an optimal method should exist for ordering the organic world. I argue that this method is the evolutionary one, as its pragmatic and theoretical bases are the most firmly tied to Darwinism and selectionist theory.

Phenetic taxonomy will be only briefly discussed, as there have been excellent critiques of the methodological and philosophical problems inherent in that system (Hull 1967, 1968, 1970, Johnson 1970). Sneath and Sokal (1973) continue the more extreme phenetic approach, but largely ignore the criticism directed at their theories of classification. The most devastating discussion of computer taxonomy (Hull 1970) is not mentioned or cited in their recent text.

Gillispie (1960, p. 261) notes that "the theory of natural selection is what turned the study of all living nature into an objective science," yet numericists advocate a taxonomy divorced from evolutionary concepts. Sneath and Sokal (1973, p. 18) even reject the fundamental ideas of the biological species and phylogenetic homology, desiring "to redefine them or possibly even dispense with them." Numericism can be viewed as an attempted retrogression to pure Baconian philosophy — the belief that facts must, in some way, be collected "objectively" and theory then developed subsequently. This philosophy has never been applied in science (Kuhn 1970) and facts can only have significance (indeed, can only be seen as facts) in relation to some theory.

Hull (1970) stressed the impossibility of separating classification from theory — even pheneticists have theories. Any scientific research must proceed hand-in-hand with theoretical considerations. "Purely phenetic classifications . . . are impossible and . . . even if they were possible, they would be undesirable . . . . The idea that an extensive and elaborate classification can be constructed in isolation from all scientific theories and then be transformed only later into a theoretically significant classification is purely illusory" (Hull 1970, p. 32).

Pheneticists (e.g., Cain 1959a, Gilmore 1951) assert that, as the largest source of error in classification is reliance on theory, one must classify neutrally. "Such a procedure would assuredly be safe, but in the extreme it is impossible . . . and in moderation undesirable" (Hull 1970, p. 34). Once again, an attempted rejection of theory in classification is met, but as Kuhn (1970, p. 79) notes, "there is no such thing as research in the absence of any paradigm [= theory]. To reject one paradigm without simultaneously substituting another is to reject science itself."

Pheneticists (Sneath and Sokal 1973 and references therein) claim that a classification must be "useful" — their criteria of usefulness being content of phenetic similarity and information retrieval. However, "classifications . . . are incapable of storing much in the way of specific information. Rather than being storage-and-retrieval systems themselves, they serve as indexes to such storage-and-retrieval systems. The information resides in the monograph" (Hull 1970, p. 28). Further, that a classification should be useful is misleading. The ends of taxonomy "are better characterized by the words *theoretical significance* than by *usefulness*. An extremely accurate scientific theory of great scope will certainly be useful, but there are many things which are useful, though of little theoretical significance" (Hull 1970, p. 50, italics original). This is not to negate numerical methods as valued tools in the construction of classification, but to reject the discipline as a theoretical framework for classifying real organisms.

ii) Principles of Biological Classification

Although it is not possible to axiomatize biological classification in the sense of Popper (1968a,b), a list of premises or principles may be suggested. The major premise is that Darwinian evolution has occurred and that classification must therefore be consistent with the inferred evolutionary history of organisms. Granting this premise, the following are suggested as the principles upon which a biological classification is to be based:

1. Categories are to be collective, uniting related organisms (monotypic taxa are to be avoided).
2. The taxonomic hierarchy is to reflect both cladistic and patristic relationships, that is, should reflect evolution (see Darwin 1859).
3. Fossil and Recent species are to be classified in one system.
4. Ancestral species existed in the past and have been sampled by the fossil record, and as such are as real and discoverable as are sister-group relationships. The existence of ancestral taxa is to be reflected in classification.

5. Taxa are to be monophyletic *or* paraphyletic at the lowest *possible* level.
6. All characters carry evolutionary, and thus taxonomic, information of differing import.
7. Phylogenetic reconstruction and classification are complementary, not synonymous.
8. Ranking of taxa is arbitrary, but not to be based on *a priori* assumptions.

The major premise is composed of two parts, the first of which can find no disagreement amongst informed biologists. The second part would, perhaps, be unacceptable to some cladists and pheneticists. The objections of the latter have been noted and those of the former are discussed below. The eight principles are not ranked in any order of importance, as their relative contributions to evolutionary taxonomy are indefinable, but linked.

The first principle, that categories are to be collective, seems well established. Mayr (1969, p. 236) observed that "the taxonomist must make every effort to keep the number of monotypic taxa as low as possible. Slightly aberrant species should whenever possible be included in the same genus as the most nearly related species." Simpson (1945, p. 231) notes "the vital fact that bringing things together is the more useful and important function of taxonomy." There is little disagreement over this concept in the taxonomic literature, with one cladist (Crowson 1970, p. 54) even suggesting a drastic lumping of genera in order that "it might become practicable to memorize all the valid generic names in quite extensive groups."

The advantages of this suggestion are doubtful, but excepting certain cases (such as the first known bird, *Archaeopteryx*) monotypic taxa are to be avoided.

The second principle follows from the premise that classification should reflect evolutionary relationships. The ways of inferring these relationships are discussed above. The phenetic school states that such relationships can be ignored *or* that they are best discovered by phenetic analysis (Sneath and Sokal 1973), whereas cladists assert that only cladistic relationships are relevant for classification. Evolutionists believe that both cladistic and patristic relationships must be used in classification (see Darwin 1859, Hull 1970, Mayr 1974, Simpson 1961).

Evolutionary theory is the paradigm under which biologists should work. This being so, classification must be consistent with our understanding of the evolutionary history of the group under study. There are two components to this history: splitting of lineages *and* structural change of lineages (Darwin's descent with modification). Neither phenetic nor cladistic analysis alone can hope to elucidate the course of evolution. Splitting of lineages is seemingly controlled by geographic isolation (on whatever level) of populations and/or natural selection (Mayr 1963). However, changes in lineages are controlled, not during or by splitting (contra Brundin 1972a,b, Eldredge and Gould 1972), but by natural selection acting within the framework of the species' genotype and the environment at every point in time. There is little observational or theoretical evidence that cladogenesis is directly linked or causal to the process of modification by natural selection. The phenomena of cladogenesis and divergence are separate, although both are governed ultimately by natural selection (Gingerich 1974, Mayr 1963, Williams 1966). To concentrate on one to the exclusion of the other is to violate evolutionary theory and to impose a false simplicity on nature.

The third principle states that fossil and Recent organisms are to be classified together. This principle needs little defence as all schools appear to accept it (Hennig 1966, Simpson 1961, Sneath and Sokal 1973, but see Patterson and Rosen 1977). Crowson (1970, p. 67) advocates "a separate classification for each era of the geological past," but this would produce an unworkable system, suited mainly to obscuring evolutionary relationships.

The fourth principle contends that ancestral species existed, that they are real and discoverable in the fossil record, and that they must be utilized in a system of classification. It has been recognized that, in order for Hennigian classification to stand, this principle must be rejected. Therefore, Nelson (1973, p. 311) has "assumed that ancestral species cannot be identified as such in the fossil record [as] . . . this assumption is fundamental to Hennig's phylogenetic systematics." It is stressed that ancestor-descendant relationships are hypothetical (Nelson 1970), but of course sister-group relationships are no less hypothetical and one should not reject either system of relationship. Rather, each situation must be judged on its own basis, using the information at hand. In some cases an hypothesis of descent from a common ancestor will be most reasonable, in others one of an ancestor-descendant relationship will be preferred. In the sense of parsimonious and realistic (that is, scientific) hypotheses, objections that ancestor-descendant relationships cannot be proved are trivial, in that science does not concern itself with proof (see Popper 1968a,b). Although imperfectly, the evolutionary approach can incorporate ancestor-descendant relationships into a classification (as well as into phylogenetic analysis), the cladistic system cannot.

It might even be disputed, theories of classification aside, whether cladistic analysis is to be preferred in all cases. Certainly when considering only Recent organisms, cladistic methods are excellent, as they do not (explicitly) attempt to force contemporaneous species into roles of ancestors and descendants. For clarity of expression, cladograms are used when applicable in my phylogenetic analysis below. However, if the fossil record is considered, it becomes unreasonable to limit oneself to analysis separated from stratigraphic data and inferred ancestor-descendant relationships, forcing all organisms into a single time plane.

Figure 91 is redrawn from Schaeffer, Hecht, and Eldredge (1972, fig. 1). It is claimed (Schaeffer et al. 1972, pp. 40-41) that "a cladogram [Fig. 91A] claims less than, but actually says as much as, a phylogenetic tree" and that "a phylogeny . . . is a theory of relationships expressed in the form: Taxa A and B are more closely related to each other than either is to C." However, neither of these assertions can be accepted. Firstly, comparison of Figure 91A and 91B makes it evident that both diagram the same theory of relationships, with no real ancestors recognized in either case. Both "claim" the same thing, but the phylogenetic tree in Figure 91B "says" a good deal more than that in Figure 91A, as the former shows known stratigraphic ranges. Comparing Figures 91A and 91C, it can be seen that the latter both "claims" more and "says" more than the cladogram. In some cases it is more reasonable to hypothesize direct ancestor-descendant relationships, and to claim less than is warranted is not scientific. Secondly, based on evolutionary theory, phylogeny is real and it is certainly not a statement of two taxa being more closely related than either is to a third. Such a statement expresses an hypothetical cladistic relationship, which hopefully conforms to some real phylogeny. Even an hypothesis of phylogenetic relationship is, in some cases, more than a statement of inferred sister-group relationships. Ancestors are real and if the evidence supports an hypothesis of ancestor-descendant relationship it is unreasonable to claim less. Whenever nature fails to conform to a model, it is not nature that is to be changed.

It is accepted by cladists and evolutionists that taxa should, ideally, be monophyletic (principle 5), although certain pheneticists have advocated that this be ignored. Sneath and Sokal (1973) attempt to have things both ways, stating that "phenetic groups are usually monophyletic" (p. 47), but elsewhere that classifying a taxon with the group with which it converges rather than with the group from which it originated "is more generally useful" (p. 57). Even in phenetic terms, the "usefulness" of such a procedure is doubtful.

A point of contention remains, however, between cladists and evolutionists. Cladists argue that a taxon must be strictly monophyletic, that is "a group of species descended from a single ("stem") species" (Hennig 1966, p. 73). If actual stem species could be recognized by cladistic taxonomists, they would have to be classified separately, with a rank equal to that of the two derived taxa (Nelson 1973). According to Hennig's definition, taxa such as the Osteichthyes, Amphibia, and Reptilia are invalid as they do not include all species descended from their (hypothetical) common ancestor. In his terms they are paraphyletic.

In evolutionary taxonomy, the criteria for monophyly are less rigid. Although the aim is to produce taxa that are monophyletic at the lowest practical level, Simpson's definition is usually followed. This states that "*monophyly is the derivation of a taxon through one or more lineages . . . and from one immediately ancestral taxon of the same or lower rank*" (Simpson 1961, p. 124, italics original). Paraphyletic taxa cause no concern, in recognition of the fact that there are patristic components to phylogeny (see Darwin 1859) and that the adaptive zone of a taxon is an important evolutionary phenomenon (see also Van Valen 1971), worthy of expression in classification. Evolutionary systematists recognize that monophyly at a low level is desirable, and this is reflected in their classifications. Nevertheless, empirical evidence and selectionist theory admit the possibility (or probability) of several lineages giving rise to a higher taxon in such a way as to be indistinguishable. "It seems more reasonable to assume that several to many phyletic lines are involved in the origin of new groups . . . . This pattern is not in conflict with any positive paleontological data, and it is in close agreement with the concepts of mosaic evolution and transitional adaptive zones, and with the diversification shown by recent groups of organisms" (Bock 1965, p. 280). Nelson's (1970, p. 383) claim that his earlier (1969) classification of the vertebrates is made up of taxa that "are, or at least seem to be, monophyletic in the strict sense of the word, i.e., at the level of the biological species" is merely an untestable hope (and most probably false).

The contention that all characters hold evolutionary, and hence taxonomic, information of one sort or another (principle 6) will find support amongst pheneticists and evolutionists, but disagreement from cladists. It is a cladistic axiom (Hennig 1966) that only apomorphic (shared-derived) characters can be used to determine relationships. In the strictest genealogical sense this is, perhaps, true, although cladists were not the first to use the principle of shared and derived characters in phylogenetic analysis. Further, plesiomorphic is a relative term (see below) and as evolutionary biologists our concern should be with all the relationships and attributes of organisms.

In Figure 92 is diagrammed a scheme of relationships between seven Recent taxa. Taxa A, B, and G are each accorded familial rank (actually the families Amphiumidae, Ambystomatidae, and Cryptobranchidae, respectively). The taxa C, D, E, and F each represent a genus (of the Hynobiidae). Block 1 represents a complex of characters hypothesized to have been present in the ancestral urodele stock and therefore plesiomorphic with respect to the taxa under discussion (although not necessarily to the Amphibia). Block 2 is a complex of characters uniting taxa C, D, E and F and believed to approximate to the characters of block 1. Therefore, if C, D, E, and F are to be united in a common family, this can only be done on the basis of characters plesiomorphic to the Caudata. Block 3 is an apomorphic complex of characters separating taxa A and B from the other taxa.

It is not known from which taxon (C, D, E, or F) that the derived groups A+B and G arose, only that they originated from taxon C+D+E+F (the Hynobiidae). Therefore, in Figure 92, the positions of C, D, E, and F are completely interchangeable. Following strict Hennigian principles, each of taxa C, D, E, and F would have to be separated into a taxon of rank equal to that of A+B (Ambystomatoidea) and G (Cryptobranchidae). However, the retention of a plesiomorphic complex of characters in the central group does indicate a common ancestry and similar selective pressures. The practicality and theoretical significance of separating each of the hynobiid genera into its own family is not intuitively obvious. It would neither reflect the evolutionary history of the group nor, given present understanding, elucidate cladistic relationships. Whether a character state is plesiomorphic or apomorphic differs according to in-group and ex-group comparisons. For example, the attainment of the nasolabial groove and lunglessness in the plethodontids is apomorphic with respect to the Caudata, but plesiomorphic when only plethodontid taxa are considered. Primitive characters have also been discussed above in the section on Phylogenetic Reconstruction.

The assertion that phylogenetic reconstruction (see above) and classification are complementary, not synonymous, processes is contentious (principle 7). Phylogenetic reconstruction and cladistic analysis attempt to infer the branching of species and higher taxa. For such studies, Hennig's (1966) principles are in many cases very useful. Classification, however, orders known species in a hierarchical system for the purposes of indexing and cataloguing, making use of inferred phylogenies and phenetic gaps. It serves as an indexed system for general reference, not in the generation of hypotheses. Real organisms and inferred phylogenies are heuristic, leading to further testable hypotheses. A list of names organized in a classification does not, in practice, serve any heuristic function.

"I believe that the *arrangement* of the groups within each class, in due subordination and relation to other groups, must be strictly genealogical in order to be natural; but that the *amount* of difference in the several branches or groups, though allied in the same degree in blood to their common progenitor, may differ greatly, being due to the different degrees of modification which they have undergone; and this is expressed by the forms being ranked under different genera, families, sections, or orders" (Darwin 1859, p. 404). The theoretical significance and practical application of a classification that exactly duplicates a cladistic reconstruction have not been satisfactorily explained. Such a system is highly unstable, changing by necessity each time different cladistic relationships are hypothesized. In an evolutionary classification, concepts of phylogenetic events can often change rather markedly, yet leave the classification untouched. Owing to the labelling and cataloguing functions of a classification, stability is most desirable, making the evolutionary system again preferable to the cladistic.

The final principle is that ranking of taxa is arbitrary. This is, apparently, not obvious. Phenetics claims to be "objective" or "non-arbitrary" by measuring similarities and ranking clusters on some unweighted mathematical basis (Sneath and Sokal 1973). However, what "similarity" is, other than a more or less intuitive judgement, has never been explained (see Hull 1970). Further, the choice of the mathematical technique must, ultimately, be as arbitrary as any judgement by a conventional taxonomist. Ghiselin (1969, p. 21) points out that "mathematics can reasonably be treated as a branch of logic, and to view any form of logic as something more mysterious or valid than what is called common sense is without foundation and smacks of the superstition of numerology. Scientific inferences should be accepted because the premises are true and because the conclusions follow logically. The truth does not derive from the jargon in which it is expressed." It is evident that the philosophical and theoretical bases of computer taxonomy are weak (e.g., Hull 1970); therefore one is not to accept their assertions merely because mathematics is used.

Cladists have attempted to rank taxa on the basis of times of splitting. This might, in theory, be nonarbitrary, but for the vast majority of organisms the fossil record is so poor as to provide few clues as to times of origin. It is true that similarities between taxa can be used to infer times of splitting, but without confirmation from fossils and stratigraphy such inferences must be weak. Selection alone directs evolution and rates of change are irregular and difficult of estimation. It is surprising that cladists tend to work with organisms lacking an adequate fossil record (Brundin 1966 [insects], Hennig 1966 [insects], Nelson 1969, 1970 [fishes]). Certain theorists have recognized this contradiction (Nelson 1970, 1973) and attempted to negate the use of fossils and stratigraphy in the reconstruction of phylogeny. Although such concepts follow necessarily from strict adherence to cladistics, they can originate only from lack of appreciation of the scientific method, of the fossil record, and of the work of paleontologists.

In order to rank taxa "objectively" on times of splitting, cladists are forced to (arbitrarily) reject the patristic component of evolution. To incorporate real ancestors and patristic features into a general purpose classification, a flexible system of ranking is needed. Raup and Gould (1974) have demonstrated that random selection and splitting can produce an ordered, seemingly hierarchical system. Brundin (1972a, p. 72) speaks of nature producing "a system of its own that is in principle hierarchic." However, this appearance is owing to our interpretation of phylogeny from the present perspective. Nature is a complex system resulting from speciation and divergence, not an ordered hierarchy. We must, therefore, attempt to produce a labelling system for this complexity — based on scientific theory and inquiry and, ultimately, a little bit of art (Simpson 1971). Ranking must be to a greater or lesser degree arbitrary and it should cause little concern that a family of insects is not equivalent to a family of salamanders. Each has been following its own evolutionary pathway for millions of years as a different kind of animal. Evolution has not made them equivalent, why should we wish to do so artificially?

"It is preferable to consider evolutionary classification not as expressing phylogeny, not even as based on it (although in a sufficiently broad sense that is true), but as *consistent* with it. *A consistent evolutionary classification is one whose implications, drawn according to stated criteria of such classifications, do not contradict the classifier's views as to the phylogeny of the group*" (Simpson 1961, p. 113, italics original). An evolutionary classification is consistent with phylogeny (both of its aspects) and therefore a reflection of evolutionary theory. It is also a stable, flexible cataloguing system, well suited to everyday use by all biologists. In these things it remains the optimal system, preferable to both cladistic and phenetic taxonomy, but capable of using the methods of both. It would seem that if Simpson (1945, 1961) were read and, more importantly, understood, fewer controversies would result. For evolutionary biologists, the logical theory of systematics must be evolutionary. Cladistic and phenetic analysis of phylogeny can be powerful tools (depending on the circumstances), but let us not confuse tools with theory or phylogenetic research with classification.

C. History of Classification of the Caudata

In order to better understand present methods and principles of classification, it is helpful to know the systems used in the past. Knowledge of the historical development of the classification of the Caudata may help reduce biases and prevent repetition of past errors. During the earlier stages of work on a higher taxon, the choice of "significant" or "meaningful" taxonomic characters is empirical and, at least in retrospect, subjective. As the group becomes better known, the classification changes and the subjective component perhaps decreases, but can never be totally absent.

The class Amphibia of Linnaeus (1758) united amphibians and reptiles, as well as lampreys, sharks and rays, and the sturgeon. These organisms were divided into Reptiles (including salamanders and lizards in the single genus *Lacerta*, all anurans in the genus *Rana*, turtles, and crocodiles), Serpentes (all snake-like tetrapods), and Nantes (the various included fishes). Somewhat later, Laurentius (1768) used three orders in a class Reptilia: Salientia (frogs and toads), Gradientia (salamanders [in two genera, *Triton* and *Salamandra*], lizards, and crocodiles), and Serpentia (snakes, apodans, and amphisbaenians).

Other classifications for the amphibians and reptiles were proposed during the late 1700's (see Kuhn 1967), but Oppel (1811) was apparently the first to place all amphibians in a single unit. This order, however, was still classified in the class Reptilia as follows:

- Class Reptilia
  - Order Testudinata (turtles and tortoises)
  - Order Squamata
    - Section Saurii (crocodiles and lizards)
    - Section Ophidii (snakes and amphisbaenians)
  - Order Nuda
    - Family Apoda
    - Family Ecaudata (anurans)
    - Family Caudata.

In modern terms the Order Nuda (= Amphibia) is natural at the higher levels: the relationship of the three included families to each other and their distinction from reptiles is clearly shown. Subsequent workers generally agreed that amphibians and reptiles were different, although both were united in a single class.

Gray (1825, p. 194) noted that the Amphibia and Reptilia "are allowed to be perfectly distinct by all modern naturalists," and divided the Amphibia as follows:

Class Amphibia
  Mutabilia (undergoing metamorphosis)
    Order Anoura
      Family Ranidae (all frogs and toads)
    Order Urodela
      Family Salamandridae (all known metamorphosing salamanders in the genera *Triton* and *Salamandra*)
  Amphineusta (lacking metamorphosis)
    Order Sirenes
      Family Sirenidae (*Siren*, *Pseudobranchus*, *Proteus*, *Necturus*)
      Family Amphiumidae (*Amphiuma*, *Cryptobranchus*)
    Order Apoda
      Family Caeciliadae.

In this classification, the presence or absence of transformation was used to divide the salamanders: one group being placed with the frogs and toads, the second comprising the fully aquatic (paedogenic) species and the caecilians. Although perhaps bizarre by present standards, given the state of the art, there was no reason to reject such a division. The theory of evolution was not available to provide an acceptable definition for a natural system of classification. Gray's classification is "good" in that it is based on observable features and in serving to distinguish subgroups of Amphibians.

Gray (1825, p. 216) placed *Amphiuma* and *Cryptobranchus* in a single family, which was defined as follows: "Branchia none, skull formed of solid bony substance; gill flaps open during life; body subcylindrical; tail compressed; legs four." Although different from present classifications, which are based on additional data and differing interpretations, Gray's Amphiumidae was based on characters that are factually correct. Only in light of our different theories and weighting of characters does the scheme become wrong.

Tschudi's (1838) *Classification der Batrachier* greatly influenced subsequent workers. He divided the Amphibia into four orders: Batrachia (frogs and toads), Cacaelia, Salamandrinae, and Proteideae. The Salamandrinae included four-footed, tailed animals, lacking external gills in the adult. The Proteideae were salamanders with elongate heads, large upper lips, external gills present or absent in the adult, and a laterally compressed tail. These two orders were subdivided as follows (modern generic and specific names substituted as necessary);

Class Amphibia
  Order Salamandrinae
    Family Salamandrae (tail round or roundish)
      Content: *Hynobius naevius*, *Onychodactylus*, *Ambystoma maculatum*, *Plethodon*, *Eurycea*, supergenus *Bolitoglossa*, *Salamandra*, *Salamandrina*.
    Family Tritones (tail laterally compressed, often high)
      Content: *Hynobius nebulosus*, *Ambystoma jeffersonianum*, *Hydromantes*, *Hemidactylium*, *Pseudotriton*, *Cynops*, *Triturus*, and their allies.
    Family Tritonides (head flat and robust; eyes small; tail laterally compressed)
      Content: *Cryptobranchus*.
  Order Proteideae
    Content: *Ambystoma mexicanum*, *Amphiuma*, *Necturus*, *Proteus*, *Siren*, *Pseudobranchus*.

Although there is inconsistency in the separation of the Salamandrae from the Tritones, the classification is "good" in terms of providing taxa that are otherwise well differentiated.

Fitzinger (1843) placed amphibians in one of five Series within the class Reptilia. Following Gray (1825), he united caecilians and some of the salamanders in a single order. Although Fitzinger did not diagnose the amphibian taxa, the names of the subsections provide clues to the reasoning used: His classification is as follows:

- Class Reptilia
  - Series Dipnoa (= Amphibia)
    - Order Batrachia (frogs and toads)
    - Order Hemibatrachia (transforming salamanders)
      - Section Phaeneropleurae
        - Family Pleurodelae
          - Content: *Pleurodeles.*
      - Section Cryptopleurae
        - Family Salamandrinae
          - Content: *Salamandrina*, *Cynops*, *Euproctus.*
      - Section Geophili
        - Family Salamandrae
          - Content: some hynobiids, some *Ambystoma*, most of the then known plethodontids, *Salamandra.*
      - Section Hydrophili
        - Family Tritones
          - Content: some *Hynobius*, *Ambystoma jeffersonianum*, *Pseudotriton*, *Triturus.*
    - Order Ichthyodea
      - Section Hemisalamandrae
        - Family Megalobatrachi
          - Content: *Cryptobranchus scheuchzeri*, *C. japonicus.*
      - Section Derotremata
        - Family Salamandropes
          - Content: *Cryptobranchus alleganiensis.*

Family Muraenopses
Content: *Amphiuma.*
Section Anura (caecilians)
Section Branchiata
Family Necturi
Content: *Ambystoma mexicanum*, *Necturus.*
Family Sirenes
Content: *Siren*, *Pseudobranchus*, *Proteus.*

Hallowell (1856) classified the caducibranchiate salamanders (those losing the gills at metamorphosis) in nine families, based largely on the structure of the tongue. This arrangement was as follows (Hallowell 1856, pp. 10-11, modern generic and specific names substituted when necessary);

Group A, having longitudinal teeth on the palate:
Family Salamandridae ("Tongue rather large, attached in front and posteriorly, free at the sides; toes 4-5.")
Content: *Salamandra.*
Family Seiranotidae ("Tongue well developed, oblong, rounded in front and almost truncate posteriorly, *free in its posterior half*, less so laterally, attached in front, toes 4-4.")
Content: *Salamandrina.*
Family Pleurodelidae ("Tongue small, subcircular, *free posteriorly*, and at sides, attached in front; toes 4-5.")
Content: not given.
Family Tritonidae ("Tongue fleshy, papillose, well developed, *attached in front and behind*, free at the lateral edges; toes 4-5.")
Content: *Triturus*, *Euproctus*, *Notophthalmus*, *Taricha*, the Asian newts exclusive of *Tylototriton.*
Family Ellipsoglossidae ("*Tongue oblong oval, free at the sides only*; toes 4-5.")
Content: *Hynobius.*

Group B, having transverse and longitudinal teeth on palate:

Family Plethodontidae ("Tongue broad oval, well developed, free at its lateral edges and posteriorly, attached in front; toes 4-5.")

Content: *Plethodon*, *Aneides*, *Desmognathus*.

Family Bolitoglossidae ("Tongue of moderate size, *mushroom-shaped, supported by a central pedicel*; toes 4-5 and 4-4.")

Content: *Batrachoseps*, *Pseudotriton*, *Hydromantes*, *"Spelerpes"* (remainder of the free-tongued plethodontids).

Family Hemidactylidae ("Tongue oval, attached in front and along the middle, more free posteriorly; toes 4-4.")

Content: *Hemidactylium*.

Group C, only transverse teeth on the palate:

Family Ambystomidae ("Tongue ovate, moderately free at its edges, slightly so in front, attached posteriorly; toes 4-5.")

Content: *Onychodactylus*, *Ambystoma*, *Dicamptodon*.

Hallowell classified the families on the basis of the disposition of the teeth on the palate. The Hynobiidae, some species of which have transverse rows and others longitudinal rows of teeth, were not recognized. Except for this, and the splitting of the presently recognized Salamandridae into four and the Plethodontidae into two families, Hallowell classified the Caudata in groups considered natural today.

In a second classification, Gray (1858) noted the variability of external features in salamanders and used cranial structure as the major diagnostic character complex. This, by implication, indicates recognition of the necessity for weighting characters. Gray considered the frontosquamosal arch of major importance for a natural classification of the Caudata. He divided the Salamandridae of present usage into three families, erected the Molgidae for *Hynobius naevius*, and placed ambystomatids, plethodontids, and the majority of hynobiids in the family Plethodontidae.

In the following year, Cope (1859) published a classification of the caducibranchiate salamanders as follows:

Order Caducibranchiata (gills lost at metamorphosis)
  Suborder Urodela
    Family Protonopsidae ("Branchial apertures persistent.")
      Content: not given.
    Family Salamandridae ("Branchial apertures none.")
      Subfamily Ambystominae (lacking "parasphenoid" teeth, palatine teeth in a transverse series on elevated parts of the vomer)
        Content: *Onychodactylus*, *Cryptobranchus japonicus*, *Ambystoma*.
      Subfamily Spelerpinae (numerous parasphenoid teeth, plus a short transverse series of vomerine teeth)
        1. Plethodontae (tongue attached)
          Content: *Plethodon*, *Aneides*, *Desmognathus*.
        2. Spelerpeae (tongue free)
          Content: free-tongued plethodontids.
      Subfamily Hynobiinae (vomerine teeth said to be lacking, "parasphenoid" teeth in two anteriorly diverging rows)
        Content: *Hynobius*.
      Subfamily Salamandrinae (vomerine teeth on inner surfaces of vomers, which are elongate and posteriorly divergent)
        1. Salamandrae (vomerine teeth "cuneiform," ribs claimed lacking)
          Content: *Salamandra*.
        2. Pleurodelae (vomerine teeth "cuneiform," ribs large)
          Content: *Salamandrina*, *Pleurodeles*.

3. Tritones (vomerine teeth "cuneiform," ribs claimed lacking)

Content: remainder of the newts then recognized.

Cope wrote (1859, p. 122) that: "The characters of the . . . subfamilies are taken from the position, etc., of the palatine and sphenoidal teeth, and we are of the opinion that the groups thus formed will be found to be more natural than those established exclusively upon the form of the tongue." These characters did serve to separate the metamorphosing salamanders into more or less their presently accepted families (called subfamilies by Cope). While arguing that his classification was more "natural" than those based only on the "form of the tongue" (probably a reference to Hallowell 1856), Cope was not explicit as to what "natural" might mean.

Having chosen the presence or absence of gill slits in the adult as the character used to separate the Urodela into two families, Cope (1859, p. 122) was forced to place the cryptobranchid species into two different families, stating that "the great aquatic salamander of Japan is closely allied to our *Protonopsis* [= *Cryptobranchus alleganiensis*] . . . but the absence of branchial slits places it among the true Salamanders." This is, at least, consistent and selection of characters is difficult in the absence of evolutionary theory.

Cope (1867) published a more detailed and rigorous classification, which was based on a series of primarily osteological characters. Cope criticized the use of Perennibranchiata (gilled adults) and Caducibranchiata (gills lost at metamorphosis), noting *Siredon* (= *A. mexicanum*) was known to metamorphose into *Ambystoma*, the resemblance of *Necturus* to larval plethodontids, and the variable development of gills in *Siren*. He recognized that separation of the caducibranchiates into those with and without gill slits (as he had done previously [Cope 1859]) was not justified, stating that "this feature is of no greater value than any other, as the very closely allied genera *Protonopsis* [= *C. alleganiensis*] and *Megalogatrachus* [= *C. japonicus*] differ in this respect" (Cope 1867, p. 104). Cope's order Urodela included three suborders: the Trachystomata (for the Sirenidae), Proteida (Proteidae), and Caducibranchiata (the remaining families). Of the Caducibranchiata, Cope (1867, p. 102) stated: "This name, although not strictly applicable to Siredons included in the suborder may be retained." Caducibranchiate salamanders were divided into eight families as follows:

A. Family Amphiumidae (as presently recognized)
B. Family Protonopsidae (= Cryptobranchidae)
C. Family Amblystomidae (= Ambystomatidae plus *Onychodactylus*)
D. Family Plethodontidae (as presently recognized, exclusive of the Desmognathini)
   Family Desmognathidae (= Desmognathini)
E. Family Hynobiidae (as presently recognized, minus *Onychodactylus*)
F. Family Salamandridae (*Salamandra, Triturus cristatus*)
   Family Pleurodelidae (= Pleurodelinae, minus *T. cristatus*).

In comparison to this classification, that of Boulenger (1882) represents in retrospect a major regression. Boulenger separated the order Caudata into four families: the Proteidae and Sirenidae were as presently recognized; the Amphiumidae included *Amphiuma* and *Cryptobranchus*; and the Salamandridae was divided into four subfamilies. The Amphiumidae were distinguished on the absence of external gills and eyelids in the adult, the presence of maxillae, and the possession of amphicoelous vertebrae. The Salamandridae were divided as follows:

1. Salamandrinae (= Salamandridae as presently recognized)
2. Amblystomatinae (Hynobiidae and Ambystomatidae)
3. Plethodontinae (Plethodontinae of Wake 1966)
4. Desmognathinae (Desmognathinae of Wake 1966).

Although different from those of today, these older classifications are constructed in a similar manner. Characters that are distinctive and allow for the separation of species into more or less well-defined groups continue to be used in classification. Although we have the theory of evolution as a unifying principle, many taxonomic characters are still chosen on an empirical basis (see Darwin 1859). The old classifications should not be viewed in the context of our present, "correct" systems as naive attempts to order salamanders. They must be judged on their own merits as to whether they are internally consistent and follow from data then available. On this basis, many of the older schemes are admirable. After Boulenger (1882), who can be taken as the last of the old taxonomic school, the classifications become more recognizable.

Cope (1889) proposed a modified classification in his report on *The Batrachia of North America*. Three orders were used to hold the subordinate taxa, whereas one had been sufficient previously (Cope 1867). This classification is as follows:

1. Order Urodela
    - Suborder Apoda
    - Suborder Trematodera
        - Family Cryptobranchidae
    - Suborder Amphiumoidea
        - Family Amphiumidae

- Suborder Pseudosauria
  - Family Amblystomidae
  - Family Hynobiidae
  - Family Plethodontidae
  - Family Desmognathidae
  - Family Thoriidae
  - Family Pleurodelidae

2. Order Proteida
   - Family Proteidae
3. Order Trachystomata
   - Family Sirenidae.

This classification does not differ profoundly from those presently in use. Cope (1889) split the Plethodontidae into three families and the Salamandridae into two. The Proteida were separated from the Urodela on the basis of the unique presence of the large opisthotic (Cope's *os intercalare*). Cope believed this indicated that proteids were intermediate between the stegocephalians and other salamanders. Sirenids were placed in a distinct order Trachystomata, which was suggested to be derived from the Urodela.

The next major contribution was proposed by Dunn (1922), in which the families are those still recognized and arrangements of the taxa are similar to those of today. The classification was based on several characters and is as follows:

- Order Caudata
  - Suborder Mutabilia
    - Superfamily Salamandroidea
      - Family Ambystomidae
      - Family Salamandridae
      - Family Plethodontidae
    - Superfamily Amphiumoidea
      - Family Amphiumidae

- Superfamily Cryptobranchoidea
    - Family Hynobiidae
    - Family Cryptobranchidae
- Suborder Proteida
    - Family Proteidae
- Suborder Meantes
    - Family Sirenidae.

Cope's (1889) continuing influence is seen in the three-way division of the Caudata into the Mutabilia (Cope's Urodela), Meantes (Cope's Trachystomata), and Proteida. Hynobiids and cryptobranchids are still placed in the Cryptobranchoidea, even though this grouping is based on primitive features. Sirenids and proteids were separated into their own suborders owing to uncertainty as to their true relationships.

Dunn (1922, p. 421) explicitly stated that "classification should be based upon all available characters, so that possible parallelisms will not lead to wrong conclusions." He (1926) subsequently modified this classification, splitting the Caudata into three suborders: the Meantes and Cryptobranchoidea, which contained the same families as before, and the Salamandroidea, into which all other families were placed.

In the *Biology of the Amphibia*, Noble (1931) provided the classification that was to stand basically unaltered until the late 1960's. He included detailed diagnoses of the suborders and families, as well as a phylogenetic reconstruction for the order (Noble 1931, fig. 145). The classification is as follows:

Order Caudata
  Suborder Cryptobranchoidea
    Family Hynobiidae
    Family Cryptobranchidae
  Suborder Ambystomoidea
    Family Ambystomidae
  Suborder Salamandroidea
    Family Salamandridae
    Family Plethodontidae
    Family Amphiumidae
  Suborder Proteida
    Family Proteidae
  Suborder Meantes
    Family Sirenidae.

Although Noble's ideas of the Salamandroidea are not accepted by present workers (e.g., Regal 1966, Wake 1966), the character used to unite them is real and readily observable. Noble (1931, p. 473) defined salamandroids as comprised of "metamorphosing urodele[s] having teeth on the roof of the palate well behind the internal nares." This is now interpreted as owing to convergence in all three families.

Laurent (1947) pointed out the fundamental difference in the situation of the vomerine teeth between salamandrids and plethodontids. Whereas salamandrids have longitudinal palatal teeth formed of posterolateral extensions of the tooth-bearing parts of the vomers, plethodontids have parasphenoid tooth patches produced by posterior migration of teeth from the medial portion of the vomer (see Regal 1966). Laurent (1947) also noted that plethodontids usually retain a septomaxillary, have well-developed costal grooves, lack a fronto-squamosal arch, and usually have amphicoelous centra; characters which differ from those of the majority of salamandrids.

In a detailed study, which has unfortunately not been published, Larsen (1963) proposed a new system of relationships for the Caudata. Following Laurent (1947), he considered plethodontids to be best referred to a separate suborder, the Plethodontoidea, derived independently from hynobiid ancestry and not closely related to salamandrids. Larsen suggested that amphiumids were derived from salamandrids, sirenids from plethodontids, and that proteids evolved from "prohynobiid" ancestry prior to the origins of the other families. The data for these conclusions primarily came from cranial osteology, although other evidence was also considered.

Monath (1965) suggested further revisions, and Regal (1966) proposed a new classification, as follows:

- Order Caudata
  - Suborder Cryptobranchoidea
    - Family Cryptobranchidae (hynobiids and cryptobranchids)
    - Family Ambystomatidae
    - Family Plethodontidae
  - Suborder Amphiumoidea
    - Family Amphiumidae
  - Suborder Proteida
    - Family Proteidae
  - Suborder Meantes
    - Family Sirenidae.

This classification is based primarily on the dispositions of the vomerine teeth, although Monath's (1965) work on the auditory apparatus supported unification of plethodontids and ambystomatids in a common suborder. Regal (1966) suggested that the Amphiumidae were probably closest to ambystomatids and plethodontids, without noting that his primary character (the vomerine teeth) would controvert such a relationship. Of note in this classification is the rejection both of breeding behavior and primitive cranial features as a basis for separation of hynobiids and cryptobranchids into a distinct suborder. Except for the relationship between ambystomatids and plethodontids, Regal's arrangement has not been accepted, undoubtedly in large part because it ignores the primary dichotomy between cryptobranchoids and the remainder of the Caudata.

Wake (1966) included a classification of the families of salamander in his study of the Plethodontidae. This differed from that of Regal in recognizing the Cryptobranchoidea in the sense of Noble (1931), including plethodontids and ambystomatids in the Ambystomatoidea, classifying *Necturus* and *Proteus* in separate families with salamandrids and (questionably) amphiumids in the Salamandroidea, and changing the name Meantes to Sirenoidea. Justification for the arrangement of the families was not provided.

Wake (1966, p. 74) suggested that the "suborders Ambystomatoidea and Salamandroidea represent separate evolutionary lines that have diverged independently from an ancestral stock similar to modern hynobiids." This statement is controverted by evidence from the vertebral column and trunk musculature (see above), and it also ignored several important shared-derived characters known at the time. Nevertheless, this classification seemed to reflect knowledge of the interfamilial relationships of the Caudata and has been the one most utilized since.

A recent reorganization of the salamanders was proposed by Edwards (1976):

Order Caudata
  Suborder Cryptobranchoidea
    Family Cryptobranchidae
    Family Hynobiidae
  Suborder Sirenoidea
    Family Sirenidae
  Suborder Proteoidea
    Family Proteidae
  Suborder Batrachosauroidoidea
    Family Batrachosauroididae
    Family Prosirenidae
  Suborder Amphiumoidea
    Family Amphiumidae
  Suborder Ambystomatoidea
    Family Dicamptodontidae
      Content: *Dicamptodon*, *Rhyacotriton*, scapherpentontids.
    Family Ambystomatidae
      Content: *Ambystoma*, *Rhyacosiredon*.
    Family Plethodontidae
  Suborder Salamandroidea
    Family Salamandridae.

The major distinctions of this classification are the new family Dicamptodontidae and the unification of batrachosauroidids and prosirenids in a single suborder. I disagree with the changes proposed by Edwards and a discussion is found below (see Conclusions).

Consideration of the historical development of the classification of the Caudata is instructive. The earlier attempts to attain "natural" classifications were necessarily based on differing philosophical standards (pre- and post-Darwinian). Multicharacter classifications based on reasoned arguments as to the relative importance of the various characters gradually developed. Early workers attempted to set up schemes based on single distinguishing characters (e.g., Gray 1825), whereas the later ones (e.g., Cope 1867, 1889) utilized suites of traits in classifying. The change was probably aided by the impact of evolutionary theory and Darwin's detailed consideration of taxonomic problems.

Darwin (1859, p. 417) wrote that "it has been found, that a classification founded on any single character, however important that may be, has always failed." He noted (p. 415) that "almost all naturalists lay the greatest stress on resemblances in organs of high vital or physiological [i.e. functional] importance. [But] . . . the mere physiological importance of an organ does not necessarily determine its classificatory value . . . [as] in allied groups, in which the same organ . . . has nearly the same physiological value, its classificatory value is widely different." The important point is constancy of development, with "a character nearly uniform, and common to a great number of forms, and not common to others, . . . [being used] as one of high value" (Darwin 1859, p. 418).

Chapter IV

CONCLUSIONS

A. Functional Morphology

i) Introduction

In this section data gained during this study are used to make suggestions as to the functional reasons for certain structures. As these hypotheses are derived almost solely from dissection of preserved material, they are tentative. Comparative anatomy as a sole or major tool in the study of function has been criticized, but I believe it to be a valuable aid.

Gans (1966, p. 46) argues that, in general, function cannot be derived from the study of structure and that: "Functional morphology on the basis of deduction from structure should then be restricted to rare animals or fossils, on the assumption that it may be possible to derive some information from "similar" forms." This is basically correct, but in practice comparative anatomy would seem to necessarily come before functional morphology. That is, the first step in functional morphology is the formulation of hypotheses from information based on the study of structure (see Regal and Gans 1976, Lombard and Wake 1976, for such preliminary steps).

Gans (1966, p. 45) states that there are three assumptions to be accepted in order to allow (in theory) elucidation of function from structure. These are as follows:

"(1) that the architecture of an element is molded primarily by present function,

(2) that a given structure is in the grip of a single over-riding function, and

(3) that a structure will incorporate an equal factor of safety (or no factor of safety) in all directions and versus all kinds of adaptation induced stresses."

Gans then argues that each of these assumptions is invalid, which is partially correct. I would also agree that definitive functional morphology is not possible based only on comparative anatomy of preserved material. However, comparative anatomy must come prior to studies of living animals, so as to elucidate potential functional relationships, which can then be tested.

Whereas it cannot be argued that detailed functional interpretations can be based solely on structure, it is possible to arrive at relatively detailed hypotheses from strictly structural studies. It is reasonable, I suggest, to assume "that the architecture of an element is molded primarily by present function" (Gans 1966, p. 45), so long as the statement is qualified. Dichotomy of structures into those owing to immediate adaptation and those owing to descent is all but completely artificial, as shown by Cain (1964). All existing structures are, to a greater or lesser extent, owing to descent, but also, almost invariably, to immediate functional requirements. Retention of a structure derived from some ancestor is based on continuing selection, loss of function leading to loss of the structure. Historical factors are extremely important, but not because they force a lineage into inadaptive or suboptimal states. Structures and functions already present necessarily influence and canalize future change by their interactions with natural selection, but the first assumption of Gans is still very reasonable.

The validity of the other assumptions depends on the role that is assigned to the elucidation of function from structure. Gross errors are possible, and small errors inevitable, if it is attempted to deduce all possible functions from the structure of a system. However, there is surely no need to assume (operationally or theoretically) a one structure-one function relationship. If it is recognized that structures often have multiple functions, comparative anatomy remains a powerful (and indispensable) tool in the study of function.

Comparative anatomy allows one to understand what structures are present and to formulate generalizations and hypotheses of probable actions and functions. "Partitioning the several kinds of similarities [homology, analogy, and homoplasy] is likely to be most successful when one is simultaneously comparing as many members as possible from what appears to be a single adaptive radiation" (Gans 1974, p. 18). On this basis, the sort of functional morphology advocated by Gans (1966, 1974) may then be carried out.

Gans' (1974) *Biomechanics* exhibits this approach very well, perhaps in contrast to his more theoretical treatment published earlier (Gans 1966). It incorporates functional studies on "intact" animals as well as detailed considerations of structure. Regal and Gans (1976) provided comparative anatomical descriptions of frog tongues. Such a study and its functional speculations then serve as the first step prior to more detailed functional studies (see also Lombard and Wake 1976).

Studies such as mine on the trunk musculature and vertebral column of salamanders potentially open further possibilities for functional morphology. Elucidation of how species of different genera and families differ structurally allows comparison of their natural histories and inferences of possible explanations and correlations. These can then be tested and expanded by studies of living animals, as urged by Gans (1966, 1974). Unless one knows precisely what structures are present and their intra- and interspecific variations, experimental functional morphology, even if possible, is sterile.

ii) Interpretations

Transverse processes and ribs.- Noble (1931) proposed that bicipital ribs in salamanders function to resist the downward pull of gravity on the viscera in terrestrial situations. Certain facts seem to support this suggestion: for example, aquatic salamanders tend, on average, to have closely appressed rib-bearers (e.g., *Cryptobranchus*). However, other facts stand in contradiction. Frogs lack bicipital ribs and rib-bearers, usually retaining only somewhat elongated transverse processes. In these animals the belly hangs down as a large bag, supported by only a small amount of lateral and ventral abdominal musculature. Also, rather than being oriented vertically, as in salamanders, these transverse processes are more or less horizontal and dorsoventrally flattened. In salamanders the ribs and rib-bearers are almost invariably most bicipital anteriorly, in the region of the pectoral girdle. In the posterior region of the trunk, where the viscera are concentrated, they are generally less strongly bicipital.

Musculature would seem sufficient to hold in the contents of the abdominal cavity. Finally, it is to be noted that the ribs are usually completely enclosed within the *dorsalis trunci* and *subvertebralis*, which indicates that ribs do not function directly in support of the viscera. Lizards, which are more fully terrestrial and often much larger than salamanders, do not show the bicipital ribs and transverse processes seen in urodeles.

I suggest a different explanation for the presence of long rib-bearers and bicipital ribs: in salamanders the transverse processes and ribs are functioning as integral parts of the myosepta separating the myomeres. The transverse processes and proximal heads of the ribs are oriented in conformity with the slope of the myomeres, serving as rigid (in the case of the transverse processes) or semi-rigid (in the case of the ribs) sites of attachment for muscle fibers.

Owing to the mechanism of the buccal pump in lung ventilation (Gans 1974), elongate transverse processes in salamanders are possible. This contrasts with lizards, mammals, and labyrinthodonts in which the ribs are mobile directly on the centrum without an intervening transverse process (see Romer 1966). In these sorts of animals the ribs function for costal pump ventilation as well as in locomotion. However, in salamanders the transverse processes and ribs function only in locomotion. The transverse processes align with the myosepta and the ribs form movable lateral extensions from them. Such transverse processes serve as solid sites of attachment for muscle fibers so as to allow for short bursts of rapid movement. Urodeles spend much time at rest, moving quickly and suddenly only to capture prey (when in the water) or to escape predation. Movement is often rapidly initiated and quickly terminated. Similar habits are also exhibited by the fish *Amia* and *Lepisosteus*, both of which also have transverse processes.

This model should have significance for inferences about Paleozoic amphibians. The sort of rib articulation should indicate whether a buccal or costal pump was being utilized, and allows inferences as to how the organisms were living. Unfortunately, such suggestions are often made on the basis of little, or incorrect, evidence from living organisms.

Opisthocoely (see Figs. 93-97).- There has been no satisfactory hypothesis proposed to account for the presence of amphicoely and opisthocoely in the different families of salamanders. The problem may be considered in two parts:

1. Why are some salamanders amphicoelous and some provided with a ball-and-socket intercentral joint?
2. Why are all salamanders provided with a ball-and-socket joint opisthocoelous and none procoelous?

Information from the study of the trunk musculature of representatives from all of the living families of salamanders, and of dissections of certain lizards, can be used to help answer these questions.

Wake (1966, p. 57) concluded that the "development of opisthocoely facilitates increased intervertebral movement, the result of increased trunk and tail flexures." The first part of this suggestion is partially true, the second part is controverted by various facts and overlooks certain correlations. If true, Wake's suggestion would seem to indicate that the more flexible salamanders should be opisthocoelous.

Cryptobranchids, amphiumids, sirenids, and proteids are, however, fully amphicoelous. Further, it is likely that the latter two families are derived from opisthocoelous ancestors (see below), being secondarily amphicoelous.

Snakes might superficially seem to provide support for Wake's theory. However, these reptiles require a column that is both flexible and strong, therefore requiring smooth ball-and-socket joints. An amphicoelous snake, although highly flexible, would lack the strength necessary for such a relatively large, active, terrestrial vertebrate. Snakes also have numerous, rather short vertebrae to increase flexibility. Among fish, only the relatively rigid gar-pike (*Lepisosteus*) has non-notochordal vertebrae (which are opisthocoelous).

Data from anurans also controvert the suggestion that the ball-and-socket joint in amphibians is to increase flexibility. These amphibians have developed a rigid column owing to the pressures imposed by saltatory locomotion. During the jump the column must be held stiff, allowing force to be concentrated in one direction (i.e., a flexible arrow is nonfunctional). Therefore, the column is strengthened by ball-and-socket joints and long transverse processes. Although the ascaphids have amphicoelous vertebrae, this exception further strengthens the argument. *Ascaphus* and *Liopelma* frequent streams, being highly aquatic and indifferent jumpers. *Ascaphus* is "sluggish," a poor jumper, and swims "rather slowly, frequently using . . . [the] hind legs alternately" (Stebbins 1962, p. 90).

I suggest that the primary factor causing selection for a ball-and-socket joint has been (and is) the need for strength, not flexibility. The system can certainly maintain flexibility, but this is not the reason for its initial development. This contention is supported by several lines of evidence from the Caudata.

The highly flexible, aquatic salamanders are invariably amphicoelous, with relatively large amounts of trunk musculature. The trunk musculature of amphicoelous species is generally also constructed so as to displace the area of contraction laterally, away from the column. This is part of the function of the marked folding of the septa of the *subvertebralis* and *dorsalis trunci* in most amphicoelous species, which is carried to an extreme in the anguilliform *Amphiuma* (see Figs. 28, 29, and 30). In this manner the force of contraction is displaced so as to decrease the direct pull on the vertebral column and thus reduce the strain on each intercentral joint.

By contrast, those urodeles that develop opisthocoely have a more direct association of musculature to individual vertebrae and a marked decrease in the amount of septal folding. Structural mechanisms to decrease strain on the intercentral joints are reduced or lacking. Individual muscle sections tend to insert discretely on the vertebrae, at which points accessory projections for origins and insertions are often developed. For example, *Desmognathus* has well-developed posterior basapophyseal muscles, pterygapophyseal muscles, and hyperapophyseal muscles (see Fig. 67), as well as the associated structures on the vertebrae (see Figs. 1 and 16). This genus also has an anterior hyperapophyseal projection situated between the posterior basapophyses of the next anterior vertebra, seemingly to augment the condyle in preventing intercentral dislocation. The salamandrid newts exhibit marked reduction in the complexity of the *subvertebralis*, the fibers being strictly intervertebral with no overlap, and the *transversus* inserting medially on the centra. Newts reduce the complexity of the *dorsalis trunci* (compare *Taricha* and *Ambystoma*), concentrating stress more directly on the column. This concentration is also evidenced by the high neural crests, aliform processes, and associated musculature. Although *Siren* is very similar in these features to the newts, it differs in the larger mass of axial musculature burying the column and, presumably, cushioning the joints. Newts show remarkable convergence in the structure of the *transversus* and *subvertebralis* with the procoelous lizards (see Fig. 97).

In amphicoelous species having anterior basapophyseal musculature, the anterior basapophyseal muscles are generally not intimately attached to the anterior basapophyses. These muscles are loosely connected to the centrum medially and are probably more properly part of the posterior (transverse process) flexures in a functional sense. By contrast, urodeles with posterior basapophyseal muscles (derived from the posterior flexures) tend to have well-developed, sometimes greatly enlarged, posterior basapophyses. The muscles associated with these projections are more differentiated in the sense of being separated from the more lateral parts of the *subvertebralis*, placing more direct pull on the vertebrae and intercentral joints than is the case in salamanders with anterior basapophyseal musculature.

Amphicoelous salamanders are generally highly aquatic, short-bodied, provided with relatively bulky trunk musculature, and/or relatively small. These factors indicate a lessened strain on the intercentral joints. Certain plethodontids show development of a so-called "functional" opisthocoely in larger, older individuals (see Moore 1900). In such cases the anterior cotyles extend partially into the posterior cotyles of the associated vertebrae. This suggests that the change in vertebral articulation ontogenetically occurs owing to the necessity for strengthening the joints against disarticulation. Certainly there can be no increased demand for flexibility as the animal gets larger, nor could the kind of joint produced provide for increased flexibility.

By contrast, desmognathines have a fully developed, true opisthocoely (Moore 1900). This condition in relatively small-limbed, elongate animals might seem to run counter to the argument being developed. However, the habits, cranial osteology, and musculature of these salamanders show adaptation to burrowing (see Hinderstein 1971, Wake 1977). I have observed adult *Desmognathus fuscus* displace relatively large rocks as they move under them. It would seem reasonable that the vertebral column and its associated musculature are co-adapted with the skull and correlate with these habits. Although the column is certainly flexible, there has also been selection for its strengthening, as shown by the accessory processes on the vertebrae. In this case, in order to maintain flexibility and to strengthen the column, opisthocoely has developed. This is, however, not owing to need for increased flexibility.

The conditions obtained in the extinct batrachosauroidids (including *Prodesmodon*, see Naylor 1978a) might seem difficult to explain. The paedomorphic skull, elongate body (where known), and small limbs might be interpreted as more properly associated with amphicoelous centra. However, it is probable that batrachosauroidids were burrowers. There are stalked occipital condyles on the skull (see Estes 1969a, 1975), as in *Desmognathus*, and the atlas bears resemblances to that of *Amphiuma*. This indicates well-developed cranio-mandibular musculature and powerful dorsoventral movements of the head. The elongate body and small limbs (where known) are also traits correlated with burrowing. Finally, there is a good structural cline leading through the condition of the vertebrae in *Prodesmodon* and *Opisthotriton* to that of *Palaeoproteus* and *Batrachosauroides*, documenting reduction in the relative size and strength of the opisthocoelous ball. If this can be taken to reflect an actual phylogenetic event, it could indicate evolution away from a primarily burrowing way of life towards a more strictly swimming existence and, therefore, the reduction of opisthocoely.

In hynobiids, cryptobranchids, ambystomatids, proteids, and certain plethodontids, the vertebral column functions as a sort of special "notochord." That is, there is relatively little direct pull on the vertebrae. This is indicated by the dissections described above and by the general lack of distinct accessory projections from the vertebrae. In these salamanders, the column appears to be bent in a more gentle arc during locomotion than is the case in newts, as indicated by observations on living *Taricha* and *Ambystoma* and by study of preserved specimens that have been fixed in various attitudes. In addition, the structure of the axial musculature with respect to the number of flexures and the amounts of musculature suggests adaptations to concentration of pull away from the column. In salamandrids with greater amounts of trunk musculature and relatively more distinct flexures, the ball-and-socket joints of the centra are weakened (e.g., *Salamandra* and *Pleurodeles*).

By contrast, in *Amphiuma*, *Siren*, and most newts the column is a more integral part of the axial musculature. That is, the myomeres are modified so as to exert more direct pull on the individual vertebrae. As a result the vertebrae of these species are more complex, with large, often robust neural crests, distinct basapophyses, aliform processes, alar processes, and/or subcentral keels. *Amphiuma* and *Siren* are fully aquatic, buoyed up by water, and possess large amounts of musculature distal to the column. Further, in proportion to body length, the vertebrae are foreshortened (compare *Cryptobranchus*), allowing greater flexibility but less strain on each amphicoelous joint. The trunk musculature of *Amphiuma* is readily derivable from that of hynobiids or ambystomatids, whereas *Siren* lacks this complexity. The epaxial and hypaxial musculature of the latter is very simple in comparison to that of *Amphiuma* and derivable only from an ancestor possessed of fully developed opisthocoely (see below). It thus documents reversion to amphicoely, presumably necessitated by the assumption of aquatic life and the need for a highly flexible trunk and anguilliform locomotion.

In the salamandrid newts there has been reduction in the amount and complexity of the trunk musculature, correlated with the development of strong opisthocoely. Newts have greater pull concentrated on the individual vertebrae and consequently greater stress on the intercentral joints. This stress has been compensated for by the development of opisthocoely. It is also of note that the condyles in newts tend to have the anterior faces flattened (thus lacking a ball-and-socket joint), which might be expected if the joint is functioning to prevent dislocation, but not if it is mainly serving to increase flexibility (see Fig. 93). It is evident from the structure of the vertebrae and associated musculature that the newt vertebral column is subject to greater intervertebral strain than is the case in amphicoelous salamanders.

Although detailed observational studies utilizing x-ray movies are needed to test aspects of this framework, several statements regarding the locomotory systems of urodeles are possible. It has been shown (Roos 1964, Edwards 1977) that a walking salamander, whether newt of otherwise, generates a standing wave. There is, however, a major distinction between the swimming of amphicoelous salamanders (e.g., *Ambystoma*) and opisthocoelous ones (e.g., *Cynops*), although *Desmognathus* is a special case, being more similar to the amphicoelous salamanders. My observations indicate that in *Ambystoma* swimming involves holding the limbs against the sides and throwing the trunk and tail into waves. Swimming is sub-anguilliform, the entire body taking part. By contrast, *Taricha* and *Cynops* keep the trunk rigid during swimming, the propulsion coming from the relatively elongate, laterally compressed tail. In water, newts (*Cynops*, *Paramesotriton*, *Taricha*, and *Notophthalmus*) move primarily by walking: the column is held stiff and the limbs are used to push gently against the substrate.

The facts presented above indicate that the ball-and-socket joint is correlated with the necessity to develop a strengthened intercentral joint. Although it maintains and may even increase flexibility, this has not been the primary reason for its evolution.

The second question, however, remains: why are no salamanders procoelous? This problem has proven open to study by means of comparative anatomy. In discussing opisthocoely and procoely in frogs, Spinar (1972, p. 184) suggested that the deciding factor "is whether the [neural] arch of a particular species connects during ontogeny with the cranial or caudal part of the future vertebra." He also noted that Fick's (1904) rule, to the effect that "the fossa always develops on the side of the joint where the tendons of the muscles are closer to the joint, but the head on the other hand develops on that articulating element which bears the tendons more distal from the joint," could be used to help explain the development of procoely and opisthocoely. Spinar (1972, p. 183) claimed that: "As a result of different locomotory specializations, procoelous vertebrae developed mostly in the forms adapted to life on dry land but opisthocoelous ones developed in those which adapted themselves to permanent life in the water."

Positioning of the neural arch during embryological development only explains how opisthocoely and procoely develop. The "why" part of the question concerns evolutionary origins and functional reasons. There does appear to be a broad correlation of procoely and opisthocoely with terrestrial and aquatic locomotion respectively, but it is likely that this is spurious. Fick's rule, however, fits extremely well with the observations gained from dissections of salamanders (see above) and is consistent with the structure of lizards and snakes. In general, this aspect of Spinar's (1972, fig. 80) theory of the origins of opisthocoely accurately reflects the situation in salamanders that have become opisthocoelous. Posteriorly directed pull on the edges of the posterior cotyles leads to development of opisthocoely when it is necessary to strengthen the intercentral joints. This is as should be expected, with the cap (posterior cotyle) being pulled over the ball (anterior condyle).

However, Spinar's suggested origin of the procoelous condition is less satisfactory. That is, he figures tendons extending posteriorly from the anterior cotyles. In this case there would not be the same degree of force developed (in comparison to having the "tendons" extending anteriorly, as in many salamanders and at least some snakes) about the joint, and the development of procoely from such a situation is difficult to conceive. Snakes have well-developed tendons, arranged with pinnate muscle fibers, extending anteriorly from each vertebra (personal observation), in a situation analogous to that in salamanders with anterior basapophyseal muscles. Procoely, therefore, develops when there is anteriorly directed pull on the anterior cotyles.

Ambystoma maculatum, with anterior basapophyseal musculature, has a sort of "proto-procoelous" condition. The posterior cotyles are somewhat smaller in diameter than the corresponding anterior ones in larger individuals, although the condition remains fully amphicoelous. Why have not any hynobiids or ambystomatids developed procoely? Such questions are difficult to answer, and usually all that may be said is that it was not advantageous to do so. Also, the situation in these families is such that the amount of direct pull on the anterior edge of each centrum is reduced by the close association of the anterior basapophyseal muscles with the transverse process flexures and by the amount of axial musculature, thereby reducing the intercentral stress.

Figure 94 shows the basic septal pattern of the *subvertebralis* in several more primitive salamanders. *Ambystoma jeffersonianum* has the basic, presumably primitive, pattern, from which the *subvertebralis* of other salamanders can be derived. *Amphiuma means* represents a slight modification of this pattern, simply accentuating the development of the flexures. *Plethodon jordani* is an excellent structural intermediate between the more primitive families, and those showing propensity to development of opisthocoely. It has suppressed the internal row of muscle fibers of the anterior basapophyseal muscle, but retains the latter's septum. This septum and the posterior flexure now act on the posterior edge of the posterior cotyle, however. *P. glutinosus* simply represents a continuation of this trend, with more intimate association of the posterior flexure with the posterior basapophyseal area of the centrum.

Figure 95 shows the subvertebral patterns of the more derived plethodontids: the Euryciini, Desmognathini, and an extreme form found in some Bolitoglossini and Plethodontini. *Gyrinophilus*, *Pseudotriton*, and *Desmognathus* form a clear morphocline in terms of the structure of the *subvertebralis*, leading toward development of a distinct posterior basapophyseal muscle and correlated strong opisthocoely. *Batrachoseps attenuatus* shows complete suppression of the subvertebral flexures in a manner convergent upon salamandrids, but without the presence of opisthocoely or the migration of the origin of the *transversus* onto the centra. Why *Batrachoseps* has not developed opisthocoely as in the newts is uncertain, but perhaps it has something to do with the small body and thin trunk.

Figure 96 shows the subvertebral systems of *Necturus* and *Salamandra*, both of which have posterior flexures. However, these are not in close association with the centrum and do not form posterior basapophyseal muscles. In *Salamandra* opisthocoely is retained, whereas *Necturus* is amphicoelous, probably owing to reversion. Figure 97 diagrams the pattern seen in salamandrid newts as represented by *Triturus helveticus*. Subvertebral flexures are lacking, the amount of musculature is reduced, and the *transversus* originates along the ventrolateral edges of the centra. This is almost precisely the situation seen in lizards (see Fig. 97), even though the latter are procoelous. This may indicate that the exact position of the ball-and-socket joint (procoelous or opisthocoelous) is not critical. What matters is the sort of musculature present when it was necessary to strengthen the intercentral joint. *Siren* (Fig. 97) exhibits a pattern that is almost certainly derived from that seen in newts. A false anterior basapophyseal muscle has been developed from muscle fibers attaching along the front of each anterior lamella. However, the *subvertebralis* is otherwise simple and the *transversus* originates along the lateral edges of the centra and ventral lamellae. The vertebral column of *Siren* is cushioned in a large amount of axial musculature, which is, however, of simple structure.

B. Phylogenetic Reconstruction

i) Introduction

In this section the phylogenetic relationships of the families of salamanders are discussed and reasons put forth to support the proposed phylogeny. Each family is considered in turn, previous theories of relationship discussed, and conclusions reached. Intrafamilial phylogenies are reconstructed, usually by means of cladograms. This is not done because of acceptance of cladistic principles of classification (see above), but because cladistic representation is the most reasonable when dealing with organisms from a single time (the Recent). Cladistic representation failed, however, when it came to diagramming the familial phylogeny of the entire Caudata. In this case a standard phylogenetic reconstruction was used.

I have attempted to make use of evidence from as many sources as possible, considering the negative as well as the positive data. After the relationships of each family to the other families have been discussed, a phylogenetic reconstruction for the Caudata is proposed and this is translated into a new classification.

ii) Hynobiidae Cope 1860

CONTENT. *Hynobius* Tschudi 1838, *Pachypalaminus* Thompson 1912, *Batrachuperus* Boulenger 1878, *Ranodon* Kessler 1866, *Onychodactylus* Tschudi 1838, ?*Wolterstorffiella* Herre 1939, ?*Bargmannia* Herre 1955, ?*Geyeriella* Herre 1950.

FOSSIL RECORD. *Wolterstorffiella*, from the Paleocene of Europe, and *Bargmannia*, from the Miocene of Europe, were referred to the

Ambystomatidae by Herre (1950, 1955). *Geyeriella*, from the Paleocene of Europe, was believed to be a plethodontid (Herre 1950), but the well-developed anterior basapophyses forbid such an assignment, as noted by Estes (1965b). *Geyeriella* is very similar to *Bargmannia* in the structure of the trunk vertebrae and is surely referable to the same family, whatever that might turn out to be.

Estes (1965b) suggested that *Geyeriella* and *Bargmannia* were best placed in the Ambystomatidae, but from the published figures and descriptions they fit equally well within the Hynobiidae. The elongate vertebrae with extremely robust anterior basapophyses may indicate an elongate, paedogenic salamander. It would be necessary to know the patterns of spinal nerve exits in order to make an exact familial determination. The cranial fragment of *Bargmannia* figured by Herre (1955, fig. 5) possesses a separate prootic with a well-developed anterolateral boss. This boss is a hynobiid-like feature, serving for support of the pterygoid. Also, the separate prootic, although retained in dicamptodontines, is a basic hynobiid feature. I suggest tentatively that these two genera represent early derivatives from a hynobiid stock and that they be classified within the Hynobiidae. Based on the close resemblances of the vertebrae, it is possible that the two are congeneric.

Auffenberg and Goin (1959) suggested that *Wolterstorfiella* was a hynobiid, whereas Estes (1965b) preferred to classify it as an ambystomatid. Although the rib-bearers are bicipital, they are closely appressed, as in hynobiids. As noted by Tihen (1958) and Holman (1968), the vertebrae of these two families are very similar, although the rib-bearers tend to be more closely appressed in hynobiids. In this feature, the form of the hyperapophyses, and general proportions, the vertebrae of *Wolterstorffiella* are most similar to those of hynobiids (compare Figs. 2 and 3 with Kuhn 1962, fig. 15). Therefore, on the available evidence, I provisionally classify this genus in the Hynobiidae.

If these re-classifications prove valid, the range of the Hynobiidae is extended into the Paleocene of Europe. Further study of these most interesting specimens is urgently needed to clarify their taxonomic position and to test the ideas here advanced. Except for these taxa, hynobiids are not yet known from the fossil record.

RELATIONSHIPS. The Hynobiidae were not at first recognised as a separate taxon, and the species were lumped with the Ambystomatidae (see above). It has, however, been long recognised that hynobiids are the most primitive of living salamanders (Dunn 1922, Noble 1931), being at least structurally ancestral to the other living groups. On the basis of in-group (within the Caudata) and ex-group comparisons, the following character states are considered to be primitive:

1. Premaxillae paired with short facial spines.
2. Lacrimal and septomaxillary bones retained.
2. Angular and prearticular separate in the lower jaw.
4. Columella and operculum both present in the middle ear.
5. Fertilization external.
6. Second epibranchials retained in the hyobranchium of metamorphosed individuals.

Although Dunn (1922) considered *Tylototriton* to possess the most primitive cranial anatomy among all salamanders, it is all but certain that the structure seen in hynobiids is a far closer approximation to the true ancestral condition. *Tylototriton* has a superficially archaic skull, but this "primitiveness" breaks down upon closer examination (see below).

I would add the following features to the above, previously accepted, list:

1. *Subvertebralis* with anterior basapophyseal musculature and associated transverse process (= posterior) flexures.
2. *Dorsalis trunci* with relatively long anterior flexures.
3. *Rectus abdominis* divided into two distinct units: the *rectus abdominis superficialis* and the free *r. a. profundus*, which connects the hyobranchium and the pelvis.
4. Only two layers of lateral abdominal musculature: the *obliquus externus* (*superficialis*) and *transversus*, the *o. e. profundus* and *o. internus* being absent in most metamorphosed adults.
5. Spinal nerves with intervertebral exits, except in the case of those associated with the atlas (see Edwards 1976).
6. Vertebrae relatively long and low, with amphicoelous centra and appressed rib-bearers.

The characters suggested as primitive for the Hynobiidae were chosen on the bases of several criteria. Hynobiid cranial structure is determined to be primitive on the basis of ex-group comparisons, especially with frogs and dissorophids (see Bolt 1969, Eaton 1973), thus forming one end of the morphocline. External fertilization is also primitive owing to ex-group comparisons. As regards trunk musculature, the suggested primitive states are mainly arrived at by correlating transformation series and on the basis of ontogenetic data. Other, more derived families, can be derived from hynobiids by means of paedomorphosis of the trunk musculature. It is, of course, possible that rather than being truly primitive for the Caudata certain of these features are divergently specialized. Nevertheless, it is evident that, in principle, hynobiids represent a structural grade from which the other families are derivable. While recognizing the realities of mosaic evolution and continued change in "primitive" lineages, hynobiids are here accepted as the most primitive living salamanders and truly ancestral salamanders, if known, would probably be classified in the Hynobiidae.

Unfortunately little work has been done on the relationships of the hynobiid genera and species, with Dunn's (1923a) excellent monograph remaining the first and only adequate study. Dunn considered *Hynobius* to be the "central" hynobiid from which the other genera were derived. He also attempted to relate the other hynobiid genera with individual species of *Hynobius*. The monotypic *Pachypalaminus* was suggested to be closely allied to *Hynobius vandenburghi* (= *H. nebulosus* at present) and it is sometimes classified as a member of *Hynobius* (see Thorn 1968). Dunn allied *Batrachuperus* to *H. keyserlingii*, while *Ranodon* and *Onychodactylus* were also derived from *Hynobius*. Noble (1931) followed Dunn in considering *Hynobius* as the most primitive and the other genera directly derived from it.

As noted by Noble (1931) and unfortunately still true, the life habits of hynobiids are very little known. As well, the functional significance of most of the character states are not known. This is especially true as regards cranial osteology, which differs significantly from that of most other salamanders. Systematic revision of the family is needed, as well as detailed functional studies.

iii) Cryptobranchidae Cope 1889

CONTENT. *Cryptobranchus* Leuckart 1821.

FOSSIL RECORD. As noted below, I recognize only one genus of cryptobranchid salamanders, thereby including the fossil species assigned to *Andrias* in the genus *Cryptobranchus*.

Meszoely (1967) named a new genus and species of salamander from the Eocene of Wyoming as *Piceoerpeton willwoodense*, which was based on a single fragmentary trunk vertebra. Although he assigned it to the Cryptobranchidae, Estes (1969a) later suggested that it was a member of the extinct family Scapherpetontidae. Extensive material referable to *Piceoerpeton* has been collected from the Paleocene of southern Saskatchewan (Ravenscrag Formation), including atlantes and trunk vertebrae. However, two distinct sorts of jaws are potentially referable to this material. Depending upon which elements belong with the vertebrae, *Piceoerpeton* could be the earliest known cryptobranchid or, more probably, a batrachosauroidid (Naylor and Krause, in prep.).

The other fossil cryptobranchids have been traditionally placed in the genus *Andrias* Tschudi 1837 (see Westphal 1958, Meszoely 1966), but considering the genus group in other families of the Caudata shows this usage to be unjustified. As shown elsewhere (Naylor 1978c), I believe *Andrias* to be properly a junior synonym of *Cryptobranchus*.

Tschudi (1837) described the first recognized fossil cryptobranchid as *Andrias scheuchzeri*. As noted by Westphal (1958), Holl (1831) had previously named the type specimen *Salamandra scheuchzeri*, making the proper designation *Cryptobranchus scheuchzeri* (Holl). *C. scheuchzeri* is known from the Oligocene, Miocene, and Pliocene of Europe (see Thenius 1954, Westphal 1958, 1967, 1970). North American cryptobranchid fossils from the Miocene and Pliocene are probably from a single species, *Cryptobranchus matthewi* (Cook), as shown by Meszoely (1966). These specimens have also been reported on by Cook (1917), and Tihen and Chantell (1963). *C. japonicus* is known from the Pleistocene of Japan (Shikama and Hasegawa 1962), and *C. alleganiensis* comes from the subrecent of North America (Nickerson and Mays 1973).

RELATIONSHIPS. There are probably three living species of *Cryptobranchus*: *C. alleganiensis* from eastern North America, *C. japonicus* from Japan, and *C. davidianus* from China. *C. alleganiensis* is paedomorphic in comparison to the other species, but has a similar ecological role and the structure is very similar.

Cryptobranchids differ from hynobiids in their larger size, flattening and increased ossification of the skull, the loss of the septomaxillary and lacrimal bones from the snout, and the retention of various larval features (see Noble 1931). They resemble hynobiids in retention of external fertilization, separation of angular and prearticular in the lower jaw, basic structure of the vertebrae (see Fig. 3) and trunk musculature (compare Figs. 25 and 27), and basic structure of the carpus and tarsus (see Schaeffer 1941). Dunn (1922, 1923a) recognized the close resemblance to hynobiids, noting that cryptobranchids were directly derived from the former. Noble (1931) and all subsequent workers have retained this concept, generally accepting Dunn's (1922) classification of the two families in the Cryptobranchoidea (but see Regal 1966) and this scheme is here followed.

Relationships of the known species of Cryptobranchidae are uncertain. Based on the structure of the hyobranchia (see Edgeworth 1923, Fukuda 1928), and the presence of open gill slits in adult *C. alleganiensis*, the North American species is probably a paedomorphic derivative of the species previously called *Andrias*. Meszoely (1966) showed that *C. matthewi* is probably closer to *C. japonicus* than to *C. alleganiensis*, and Westphal (1958) pointed out the close resemblance of *C. scheuchzeri* to *C. japonicus*, classifying them as a single species. As noted above, the proper assignment of *Piceoerpeton* is uncertain.

iv) Schapherpetontidae Auffenberg and Goin 1959

CONTENT. *Scapherpeton tectum* Cope 1876, *Lisserpeton bairdi* Estes 1965.

RELATIONSHIPS AND OCCURRENCES. In 1876 Cope named a new genus of fossil salamander from the Judith River Formation, Montana. In *Scapherpeton*: "Vertebrae [are] deeply biconcave, with opposed, but not continuous, foramina for the chorda dorsalis . . . . Centrum with vertically compressed, short diapophyses near the posterior extremity, a prominent hypapophyseal keel, and prolonged neural spine [= hyperapophysis]" (Cope 1876, pp. 353-354). Cope recognized four species of this genus, and also erected another genus and species, *Hemitrypus jordianus*, from the same formation.

Utilizing additional material from the Hell Creek, Lance, and Judith River (including the Oldman of Alberta) formations, Auffenberg and Goin (1959) synonymized the named species of Cope with *Scapherpeton tectum*. They assigned an atlas to this species, which Estes (1964) showed subsequently to be referable to *Opisthotriton*. In addition, they erected a new family Scapherpetonidae (emended to Scapherpetontidae, see Kuhn 1967, Estes 1969a), which was compared to amphiumids and cryptobranchids, but with no explicit statement as to possible relationships provided.

Auffenberg and Goin (1959) discussed *Hemitrypus jordianus* and referred additional material to the species (based on a broken trunk vertebra), noting (p. 8) that it differed from "*Scapherpeton* in lacking a strong midventral keel" and in the possible presence of anterior basapophyses. The possibility of synonymy was discussed but rejected as, if the two sorts of vertebrae came from a single species, it was considered that the resulting "variation along the column is more than would normally be expected on the basis of modern urodeles" (p. 10).

In his monograph on the lower vertebrates from the Lance Formation, Estes (1964) provided extensive description of *Scapherpeton*. He referred numerous elements to the vertebral material (upon which *S. tectum* is based): dentaries, maxillae, premaxillae, exoccipitals, parietals, and limb elements. Except for the perhaps problematical limb elements, Estes' associations are probably correct, as confirmed by subsequent discoveries in other localities. The other salamanders known from the Lance (and other formations) are well associated: *Opisthotriton* is known from articulated skeletons, including a complete specimen from Alberta (see also Estes 1975); *Habrosaurus* shows clear sirenid features; and the associations of cranial material with *Prodesmodon* are now understood (Naylor 1978a).

Estes (1964) classified the Scapherpetontidae in the Cryptobranchoidea: "The vertebrae ~~of~~ *Scapherpeton* are of simple type if the development of the prominent ventral keel is ignored. The simple, double-headed rib-bearers, general lack of strong muscular ridges or crests, long, slender neural spines [= hyperapophyses], and amphicoelous vertebrae probably are indicative of a relatively primitive organization" (p. 66). The distinctly bicipital rib-bearers and long hyperapophyses of *Scapherpeton* are not, however, to be expected in a cryptobranchoid, nor is amphicoely or lack of muscle crests necessarily primitive.

Estes (1964) noted that the vomers are like those of *Cryptobranchus*, and there are resemblances in the "depressed form" and short nasal spines of the premaxillae. The general shape and surface for articulation with the squamosal on the parietal are also like those of *Cryptobranchus*. The exoccipitals resemble those of cryptobranchids in general shape, the "swept-back condyles," and the large vagal and tiny hypoglossal foramina. They differ in having a large dorsal suture for articulation with the parietals (see Estes 1964 for descriptions). As regards the vertebrae, Estes (1964) held that the long hyperapophyses and position of the transverse processes were cryptobranchid-like, and that the high neural arch and hatchet-shaped neural crest were similar. He also argued that the femoral head resembled that of *Cryptobranchus*.

Estes (1965a) subsequently named and described another genus and species of scapherpetontid, *Lisserpeton bairdi*, from the Upper Cretaceous Hell Creek Formation, Montana, which was based on a trunk vertebra very similar to those of *Scapherpeton*. He noted its occurrence in the Lance Formation of Wyoming and in the upper Paleocene of Wyoming and Montana. The vertebrae were held to differ from those of *Scapherpeton* in the following features: no "ossification" within the cotyles, cotyles more rounded, vertebrae generally less robust, deep subcentral fossae, dorsal arm of rib-bearer arising from the dorsal surface of the wall of the neural arch, and well-developed zygapophyseal ridges. Atlantes (with no constriction at the base of the odontoid process), parietals, maxillae (with fewer teeth than in *Scapherpeton* and the *pars facialis* further posterior), and a vomer were referred to the species. Estes (1976) subsequently referred dentaries to *Lisserpeton* from the Paleocene of Montana.

Estes (1965b, 1969a) later reinterpreted the relationships of scapherpetontids. He noted discovery of postdentary bones referable to *Scapherpeton* in which the angular and prearticular were fused, and that the maxillae were not cryptobranchid-like in structure. These facts indicate ambystomatid (especially larval *Dicamptodon*) rather than cryptobranchid relationship as do the widely bicipital rib-bearers. At present (Estes 1969a, 1976, but see Edwards 1976) the Scapherpetontidae are classified in the Ambystomatoidea, with ambystomatids, plethodontids, and batrachosauroidids. Estes (1969a, p. 231) believed scapherpetontids to be close to the Batrachosauroididae, primarily on the basis of the common posesssion of large vertebrarterial fossae, long and robust hyperapophyses, and "general form of the centrum and neural arch." He also argued that the double canals at the base of the broken rib-bearers in Meszoely's figure (1967, fig. 1) of the type specimen of *Piceoerpeton* indicated widely separated rib-bearers, which is confirmed by the Ravenscrag material. This plus the large anterior vertebrarterial fossa, deeply amphicoelous cotyles, and robust hyperapophysis, were held to indicate that *Piceoerpeton* was a derivative of *Lisserpeton*. As noted above, referral of jaw material to the vertebrae called *Piceoerpeton* is uncertain, and the relationships of the genus remain unknown.

Estes (1975, 1976) reported *Scapherpeton* from the upper Paleocene Fort Union Formation of Wyoming and the middle Paleocene Tongue River Formation of Montana. Material from the latter formation was also referred to *Lisserpeton*, the dentaries of which have non-pedicellate teeth and resemble those of batrachosauroidids. Estes (1976) suggested that this supported the previously hypothesized relationship of scapherpetontids to the batrachosauroidids. *Scapherpeton* is also known from the Ravenscrag Formation in Saskatchewan (Naylor, in prep.).

Most recently, Edwards (1976) has reclassified *Scapherpeton* and *Lisserpeton* in a new family Dicamptodontidae, along with *Dicamptodon* and *Rhyacotriton*. This was done on the basis of the patterns of the exits of spinal nerves and the supposed similarity in vertebral structure between *Scapherpeton* and *Dicamptodon*. Although the patterns of spinal nerve foramina along the column are conformable in the four genera, this is the only detailed resemblance among them. Further, *Amphiuma* has a similar sort of pattern (see Edwards 1976). The common possession of the spinal nerve pattern is equally (or more) probably a reflection of derivation from a stock intermediate between cryptobranchoids and ambystomatines. As such, it does not necessarily indicate special relationship of scapherpetontids and dicamptodontines and, at present, it is preferable to retain the family Scapherpetontidae.

Based on the pattern of spinal nerve exits, probable presence of anterior basapophyses and correlated anterior basapophyseal musculature, fused postdentary bones, divergently bicipital rib-bearers, and long hyperapophyses, I classify the Scapherpetontidae as a separate family within the superfamily Ambystomatoidea along with the Amphiumidae and the Ambystomatidae. The cryptobranchid resemblances noted by Estes (1964) indicate relatively early divergence from the basal ambystomatoid stock, but the sequence of splitting of scapherpetontids and amphiumids (see below) is uncertain. It is probable that amphiumids share a similar, but separate, ancestry within this basal stock, thus justifying classification in the same superfamily on the principles of evolutionary systematics (see above).

v) Amphiumidae Gray 1825

CONTENT. *Proamphiuma* Estes 1969, *Amphiuma* Garden 1821.

FOSSIL RECORD. Estes (1969b) has named and described the earliest known amphiumids as *Proamphiuma cretacea*, from the Upper Cretaceous of Montana, and *Amphiuma jepsoni*, from the Paleocene of Wyoming.

Proamphiuma is also known from the Oldman (= Judith River) Formation of Alberta (Fox 1976), and the Fruitland Formation of New Mexico (J.G. Armstrong, pers. comm.).

As noted by Estes (1969b), the atlantes and trunk vertebrae of *Proamphiuma* are distinctly amphiumid, leaving no doubt as to their proper familial assignment. In comparison to those of living *Amphiuma*, the vertebrae are less extremely modified. They are somewhat elongate and delicate, with less development of the crests and processes diagnostic of *Amphiuma*, presumably indicating greater similarity to more primitive urodeles. The atlas, however, is very like that of *Amphiuma*, presumably owing to attainment of similar cranio-atlantal relationships and associated musculature (see Estes 1969b, fig. 1, also Fig. 4). Estes (1969b, p. 5) states that "*Proamphiuma* is structurally an ancestor of *Amphiuma* and there is no impediment to considering it a real ancestor, as well," which is a reasonable conclusion.

A single left dentary (UA 14316, Fig. 98) from Bug Creek Anthills, Hell Creek Formation, Montana is now referable to *Proamphiuma*. It is quite small (ca. 6.5 mm long) and of a size conformable with that expected from the known vertebrae and atlantes (collections of The University of Alberta, see also Estes 1969b). The symphseal region and part of the rear is broken off, but most of the tooth row is apparently present. The jaw is not referable to any salamander previously described from the Hell Creek or other Upper Cretaceous localities and in overall shape it is similar to dentaries of *Amphiuma means*.

The tooth-bearing flange is relatively deep and there are relatively few teeth, each being large, which are features of *Amphiuma*. Although the pedicles are all broken, positions and approximate sizes of the teeth are clearly evident from the ridges remaining. These ridges are similar to those left in Recent *Amphiuma* when tooth pedicles are broken from the dentary. An internal, horizontal shelf below the tooth row presumably held the developing replacement series. This differs somewhat from that of *Amphiuma*, in which the lower part of the dentary itself holds the replacement series. The area for the articulation of the postdentary bone is similar to that of *Amphiuma*, with the development of dorsal and ventral flanges for acceptance of the forward projection of the postdentary. *Proamphiuma* differs in lacking a distinctly raised portion of the dorsal flange, although there is a raised surface in the same position. Finally, the specimen has distinct external mental foramina, as in *Amphiuma*.

Amphiuma jepsoni is probably closely related to the living *Amphiuma*. According to Estes (1969b), the crests and keels of the vertebrae are more accentuated than is the case in *Proamphiuma*. The partial skull is noteworthy in its combination of relatively primitive (wide snout, disposition of the vomers and vomerine teeth, relatively broad parasphenoid, and relatively short maxillae, see Estes [1969b]) and derived (single premaxilla, elongate premaxillary spine, apparent loss of lacrimals and septomaxillae, dorsal concavity of the articular surface of the quadrate, and frontal surrounding the olfactory tracts, see Estes [1969b]) features. The primitive features probably correlate with the retention of a relatively broad head. The vomers are more larval and less derived than those of living *Amphiuma*. That is, the posteriorly elongate, longitudinal vomerine tooth series of *A. means* is not owing to neoteny (compare salamandrids), but to the narrowness of the skull. This interpretation is supported by the lack of participation of the pterygoid in the palatal tooth rows and by the absence of palatine teeth.

The structure of the quadrate, with the dorsally concave articular surface, and of the "prominent fossa for adductor muscle attachment . . . [and of the] blunt coronoid process" on the lower jaw (Estes 1969b, p. 9) indicate attainment of the cranial musculature and mechanics seen in living *Amphiuma*, even though the skull is much broader. This inference is supported by the structure of the atlas already present in the Cretaceous *Proamphiuma*.

The known amphiumid fossils can say little of the ultimate origins of the family. They are valuable in providing times and places of occurrence, thus providing minimum ages for the origination of the family. Nevertheless, the evidence allowing for the drawing of phylogenetic conclusions must come from study of living species in this case.

RELATIONSHIPS. Cope (1889) placed *Amphiuma* in a separate suborder, which he believed to be derived from desmognathines and, in turn, to be ancestral to apodans. There are resemblances between *Desmognathus* and *Amphiuma* in the structure of the posterior part of the skull, atlas, and certain aspects of the associated musculature, but as there are marked differences in other respects these resemblances are probably owing to convergence. Reed (1920), basing his interpretation on the auditory region, suggested a relationship to plethodontids (as did Dunn [1922, 1926]) and classified the family with plethodontids, salamandrids, and ambystomatids in the Salamandroidea. By contrast, Noble (1931) believed *Amphiuma* to have come from a salamandrid stock, while Herre (1935b) suggested a specific ancestor shared with the newts *Euproctus* and *Pachytriton*. Larsen (1963), basically using data from the cranium, also favoured a relationship with salamandrids.

Regal (1966, p. 404) separated the Amphiumidae from the Salamandroidea, placing it alone in the Amphiumoidea, "in the anticipation that future studies will demonstrate relationships to the plethodontid-ambystomatid section of the Ambystomatoidea." On the basis of enzyme analysis, Salthe and Kaplan (1966) claimed *Amphiuma* to be very close to plethodontids, with origin of this lineage in the Triassic and of *Amphiuma* from the plethodontids in the Cretaceous. This interpretation is at variance with the anatomical evidence and can be rejected. On the basis of patterns of courtship, Salthe (1967) also claimed a plethodontid relationship, but study of his data indicates that, in fact, courtship patterns are quite different between *Amphiuma* and plethodontids. Basically on spinal nerve exits Edwards (1976) derived amphiumids from a stock that led ultimately to ambystomatids, plethodontids, and salamandrids.

Elucidation of the relationships of amphiumids is difficult. It is easier to refute previous hypotheses (i.e., those of special plethodontid or salamandrid relationship) than it is to produce counterproposals. *Amphiuma* exhibits traits that generally seem to be unique specializations (autapomorphies) on a basically primitive structural plan. Evidence from Edwards' (1976) study of the patterns of spinal nerve exits and comparison of the trunk musculature of amphiumids and plethodontids prohibits any close relationship of these two families. The same holds true for the hypothesis of salamandrid relationship, but to an even greater degree.

The number of chromosomes (2n=28, see Morescalchi 1975) of *Amphiuma* is shared with ambystomatids, excluding *Rhyacotriton*. The pattern of the exits of spinal nerves is similar, although not identical, to that of dicamptodontines and scapherpetontids. Cranial structure is advanced well beyond the hynobiid stage (Reed 1920, Larsen 1963), as is the presence of internal fertilization by cloacal apposition (Salthe 1967).

The trunk musculature is highly modified, but derivable from that seen in ambystomatids. The *dorsalis trunci* and *subvertebralis*, although altered by the accentuation of certain flexures and the development of new ones (see Figs. 28, 29, and 30), is of the basic pattern seen in hynobiids and ambystomatids, but very different from that of any plethodontid or salamandrid. Of special note is the structure of the lateral abdominal musculature. The relationships and pattern of each of its components (excepting the *transversus*) are identical to the situation in *Rhyacotriton*, and very similar to that of *Dicamptodon*. This is most suggestive, as it correlates with the exits of the spinal nerves discussed by Edwards (1976).

These resemblances strongly suggest affinity with the Ambystomatoidea (excluding the Plethodontidae), but the precise phylogenetic relationships remain obscure. The following are probably the more reasonable hypotheses:

1. Amphiumids are an early, independent branch from ambystomatid ancestry, represented by *Dicamptodon* and *Rhyacotriton*. Therefore, under evolutionary principles, they are to be classified as a separate family within the Ambystomatoidea along with ambystomatids and scapherpetontids.

2. *Amphiuma*, *Dicamptodon*, *Rhyacotriton*, and possibly scapherpetontids are a monophyletic assemblage and should, therefore, be classified in a separate family or superfamily.

3. Amphiumids and scapherpetontids may share a common ancestor, but the positive support for this is slight.

At present the first possibility appears to be the most reasonable. Amphiumids are in some ways intermediate between hynobiids and ambystomatids, being most like the more primitive members of the latter. *Amphiuma* shares derived features with ambystomatids in general (elongate premaxillary spine[s], internal fertilization, and number of chromosomes) and with dicamptodontines in particular (similar patterns of spinal nerve exits and lateral abdominal musculature). Its other features (single element in the middle ear, longitudinal vomerine tooth rows, fused premaxilla, complex *dorsalis trunci* and *subvertebralis*, structure of the atlas and trunk vertebrae, ossified hyobranchium, and general structure of the skull) are independently derived. Therefore, the Amphiumidae are to be classified with the Ambystomatidae and Scapherpetontidae in the superfamily Ambystomatoidea.

vi) Ambystomatidae Hallowell 1857

CONTENT. *Ambystoma* Tschudi 1838, *Rhyacosiredon* Dunn 1928, *Rhyacotriton* Dunn 1920, *Dicamptodon* Strauch 1870, ?*Ambystomichnus* Peabody 1954.

See Table 1 and Tihen (1958) for classification and content of species groups within *Ambystoma*.

FOSSIL RECORD. As is generally true for salamanders, the record of ambystomatids is sparse. *Ambystomichnus montanensis*, from Paleocene trackways in Montana, is probably related to *Dicamptodon* and may represent the earliest known ambystomatid (Peabody 1959, Tihen 1958). Estes (1965b) notes an elongate ambystomatid from the Eocene of North Dakota, but this specimen has never been described. The presumed fossil ambystomatids from the Tertiary of Europe (*Wolterstorffiella*, *Geyeriella*, and *Bargmannia*) are discussed above, where it is concluded that they are probably hynobiids, which limits the fossil record of the Ambystomatidae to North America. Occurrences of *Dicamptodon* and *Ambystoma* are discussed above under the descriptions of the trunk musculature.

The fossil record is of little direct relevance to elucidation of the inter- and intrafamilial relationships of the Ambystomatidae.

RELATIONSHIPS. Tihen (1958), in a comprehensive study of the osteology of the Ambystomatidae, divided the family into three subfamilies: Dicamptodontinae, Rhyacotritoninae, and Ambystomatinae. The Dicamptodontinae included only *Dicamptodon* and the Paleocene *Ambystomichnus*, which is based on trackways. *Dicamptodon* retains a lacrimal and the primitive division of the otic region into exoccipital and prootic bones. The premaxillary spines are broad, but this is evidently a secondary phenomenon, as larval *D. ensatus* have narrow, elongated spines. The pterygoids have extended anteriorly to abut against the maxillae in metamorphosed individuals. The Rhyacotritoninae held only *Rhyacotriton*, a monotypic genus from western North America. It differs from *Dicamptodon* in lacking a nasal (although the lacrimal is retained), having narrow premaxillary spines, and in having greatly reduced lungs. Tihen (1958) believed these two subfamilies to be early, independent branchings from ambystomatid stock.

Tihen's Ambystomatinae contains two genera, *Rhyacosiredon* and *Ambystoma*, the latter divided into subgenera and species groups as follows:

Genus *Ambystoma*
  Subgenus *Ambystoma*
    A. mexicanum species group
    A. tigrinum species group
    A. opacum species group
    A. maculatum species group
  Subgenus *Linguaelapsus*
    (*A. cingulatum* and allies)
  Subgenus *Bathysiredon*
    (*A. dumerilii*)

A. tigrinum and its allies were considered to be the more primitive members of the genus, with the genus *Rhyacosiredon*, the *A. mexicanum* group, the subgenus *Bathysiredon*, and the *A. maculatum* group and its allies being derived from this stock. The *A. maculatum* species group and its allies (subgenus *Linguaelapsus* and the *A. opacum* group) were believed to be the most derived members of the genus.

As discussed above, Edwards (1976) created a new family Dicamptodontidae for *Dicamptodon*, *Rhyacotriton*, *Scapherpeton*, and

Lisserpeton. These genera seem to share a unique pattern of spinal nerve exits: postatlantal trunk nerves are intervertebral, whereas the postsacral nerves are intravertebral. However, the taxonomic weight of this character is problematical, and basing a classification on a single character is not without problems. It is presently preferable to retain the traditional families.

Nevertheless, Edwards' (1976) work on spinal nerves is suggestive as regards the relationships of *Dicamptodon* and *Rhyacotriton*. As the trunk musculature of the two genera is similar in presumably derived features (see Figs. 33, 34, and 35), the spinal nerves provide additional information suggesting affinity. Regal (1966) also argued that *Dicamptodon* and *Rhyacotriton* should be classified together, including them in the Dicamptodontinae. In addition to the presumedly derived features, they share several primitive features (retention of lacrimal and separate exoccipital and prootic). These shared features are sufficient to justify their inclusion in the subfamily Dicamptodontinae, which is the most primitive of the family Ambystomatidae.

Tihen (1958) suggested that *A. tigrinum* and its allies were the most primitive living *Ambystoma*. This was based on their possession of the following features:

1. "The absence of specializations found in members of the other groups" (pp. 33-34).

2. Vomer with a postdentigerous process.

3. Premaxillary spines short and broad in comparison to those of the other groups.

4. Palatine teeth always present.

5. *Os triangulare* subequally triradiate.

In contrast to Tihen's interpretations, based on osteological features, I regard the *A. tigrinum* group as derived. In comparison to hynobiids, *A. tigrinum* is decidedly more apomorphic than are members of the *A. maculatum* and *A. opacum* species groups. The so-called lack of specializations in *A. tigrinum* is, in fact, a reflection of derived simplification by means of paedomorphosis.

Vertebrae of *A. tigrinum* are short and high, with short, distinctly bicipital transverse processes, features that are larval (see Fig. 9). If the vertebrae of adult *A. maculatum*, *A. jeffersonianum*, *A. macrodactylum*, and *A. gracile* are compared with vertebrae from hynobiids (see Figs. 2, 3, 6, 7), the resemblances are readily apparent. These vertebrae are elongate, relatively low, and have long, more or less closely appressed rib-bearers. The vertebrae of adult *A. tigrinum* resemble those of larval members of the *A. maculatum* group. On the basis of in-group and ex-group comparison of vertebrae, *A. tigrinum* is most derived.

This relationship is even more evident in the trunk musculature. *A. tigrinum* possesses the full complement of *obliquus externus superficialis*, *o. e. profundus*, *o. internus*, and *transversus* in the lateral abdominal series. These muscle layers are found in larval members of the *A. maculatum* group, but adults lack the *o. internus*. The *rectus abdominis* of adult *A. tigrinum* is a single, simple band of muscle fibers extending anteroposteriorly, as is found in larval salamanders generally. Adults of the *A. maculatum* group, however, have a double *rectus abdominis* divided into a superficial and a deep portion. This double *rectus* and the lack of an *o. internus* is also seen in hynobiids (although the paedomorphic *Onychodactylus* differs), indicating the primitive nature of *A. maculatum* and its allies.

Tihen (1958) considered *Rhyacosiredon* to be an early, primitive derivative of *Ambystoma* or of a pro-*Ambystoma* stock. The partially ossified hyobranchium was held to be primitive and not owing to neoteny. The pointed teeth, "general form" of the pterygoid (said to be similar to that of the hynobiid *Batrachuperus*), possibly the low coronoid process on the prearticular, and possibly the ridge on the lingual surface of the dentary were all considered primitive. Dunn (1928), however, believed *Rhyacosiredon* to be a neotenic derivative related to *A. tigrinum* and this interpretation is the more reasonable.

Rhyacosiredon retains a larval vomer and pterygoid, as well as reduced numbers of maxillary teeth in the metamorphosed adult (see Tihen 1958). Although Tihen argued that ossification of the hyobranchium was primitive, consideration of the distribution of ossified hyobranchia throughout the Caudata does not permit this interpretation. Rather, it is seen as a derived response to the needs of a more aquatic life. Cryptobranchids, amphiumids, sirenids, and newts show ossification of the hyobranchium, seemingly in response to aquatic feeding (see also Özeti and Wake 1969, Wake and Özeti 1969). The other features presumed to be primitive by Tihen are equally, or more reasonably, explicable in terms of paedomorphosis. Furthermore, acceptance of the derived nature of *A. tigrinum* provides additional evidence against the primitive nature of *Rhyacosiredon*. This genus is best considered to be a late derivative from an *A. tigrinum*-like ancestor, and hence the most derived ambystomatid.

In light of recent work on members of the *A. tigrinum* group, the *A. mexicanum* group, and the subgenus *Bathysiredon* by Brandon (1970a,b, 1972, 1976, 1977) and previously known anatomical evidence, reinterpretation of these divisions is necessary. Brandon (1976) suggested that *A. dumerilii* (= *Bathysiredon*) be classified in the *A. tigrinum* group, and noted fertile hybrids between members of the *A. mexicanum* and *A. tigrinum* species complexes. He also pointed out difficulties in distinguishing members of the two groups, Throughout the remainder of this work the *A. tigrinum* group is used to also include those species placed by Tihen (1958) in *Bathysiredon* and the *A. mexicanum* group.

The remaining species groups (see Tihen 1958, also Table 1) contain the most primitive living species of *Ambystoma*. The structure of the vertebral column and trunk musculature (studied in *A. cingulatum*), as well as consideration of the data provided by Tihen (1958) and Krogh and Tanner (1972), indicate that recognition of a subgenus *Linguaelapsus* is unnecessary. This species complex will be referred to as the *A. cingulatum* species group.

The structure of the trunk musculature confirms Tihen's (1958) assignment of *A. opacum* and *A. talpoideum* to a single species group. Development of the *subvertebralis* and *dorsalis trunci* is almost identical and the lateral abdominal musculature is very similar (see Figs. 41 and 42). This controverts the suggestion of Krogh and Tanner (1972) that *A. talpoideum* is most closely related to *A. maculatum*. In fact, *A. opacum* and *A. talpoideum* are both derivable from the *A. maculatum* species group, but they are more similar to each other than either is to members of the latter group. Based on the descriptions and figures of the hyobranchial apparatus and its associated musculature presented by Krogh and Tanner, there is no special resemblance of *A. talpoideum* to the *A. maculatum* group that is not also shared with *A. opacum*. The supposed resemblances seen by Krogh and Tanner may well be an artifact of cluster analysis of minor proportional differences.

There is the necessity for slight modification of Tihen's (1958) *A. maculatum* species group with respect to the species *A. macrodactylum* and *A. gracile*, which were included in it. These two species are to be removed from the *A. maculatum* group and placed in a separate unit, the *A. macrodactylum* species group. Resemblances between these two species groups are owing to the retention of characters primitive for the genus *Ambystoma*, and other facts argue for separation. Morescalchi (1975, p. 347) noted "differences in the morphology of the various pairs of homologous chromosomes . . . within the same group of species (e.g., between *maculatum* and *macrodactylum* of the group *maculatum*, subgenus *Ambystoma*)." Eaton (1933, 1934) argued that *A. macrodactylum* and *A. gracile* shared a streptostylic suspensorium with *Rhyacotriton*. Other authors have denied this, but although the presence of streptostyly is problematical there are nevertheless resemblances of the suspensorium in the three species (see Eaton 1933, fig. A). Additional evidence is presented under the anatomical descriptions of *A. macrodactylum* and *A. gracile*. The *A. macrodactylum* species group is in many ways the most primitive of living *Ambystoma* and it may be occupying the ancestral area where it arose from ancestors in common with the dicamptodontines.

Based on information gained from the trunk region and cranium, and reinterpretation of previously existing data, a modification of Tihen's (1958) reconstructed phylogeny is necessary. Although the usefulness of detailed phylogenetic interpretation at the species level is generally questionable, it is possible to suggest relationships at the species group level within the Ambystomatidae.

The subfamilies Dicamptodontinae and Ambystomatinae appear to share a sister-group relationship of descent from a common ancestor (see Fig. 99). Each has retained certain primitive features and modified others. The Ambystomatinae are primitive in the structure of the vertebrae and trunk musculature, as evidenced in the *A. maculatum* and *A. macrodactylum* groups. Dicamptodontines are derived via paedomorphosis in this regard, with high epaxial myomeres extending well beyond the ribs, and anterior flexures meeting medially with their internal surfaces shifted ventrally (compare Figs. 33, 34, 35, 36, and 39). The lateral abdominal musculature of dicamptodontines is distinctly larval, with a well-developed *rectus lateralis*, four layers in the lateral body wall, and a simplified *rectus abdominis* which is also derived in being folded laterally and dorsally over the *o. e. profundus*. Dicamptodontines are also derived in the narrow *o. e. superficialis*, which is not segmented by myocommata. By contrast, in the cranium, dicamptodontines are primitive and ambystomatines more derived (see Tihen 1958).

An early dichotomy between dicamptodontines and ambystomatines is probable, with the former having been isolated to the west of the Rocky Mountains. The ancestors of the family would seem to have been of hynobiid stock (see Tihen 1958, and above), or at least from an ancestor represented structurally by living hynobiids. If Peabody (1954) has correctly referred the Montana Paleocene trackways called *Ambystomichnus* to a *Dicamptodon*-like salamander, this may date the primary ambystomatid dichotomy as a pre-Paleocene event.

After the dichotomy, the ambystomatines underwent their own divergence. Accepting that the *A. macrodactylum* and *A. maculatum* groups are the most primitive living ambystomatines, the subfamilial history becomes simpler and more reasonable than that proposed by Tihen (1958). *A. gracile* and *A. macrodactylum* are presumably primitive relicts in the western part of North America, with the species of the *A. maculatum* group having arisen from an ancestral stock that found its way into eastern North America. This interpretation is in closer agreement with the anatomical evidence and makes unnecessary Tihen's (1958) hypothesis that *A. gracile* and *A. macrodactylum* represent two separate invasions of the northwest from eastern North America. In this regard, studies of *A. tiheni* from the Oligocene of Saskatchewan indicate relationship to the *A. macrodactylum* group, not to the *A. opacum* group as suggested by Holman (1968).

The members of the *A. opacum* group are derivable from the *A. maculatum* group, as is the *A. cingulatum* group (Tihen 1958, Krogh and Tanner 1972). The exact sequence of splitting of these two derived stocks from the *A. maculatum* group is uncertain. As argued above, the *A. tigrinum* group also finds its origins in the *A. maculatum* group and, in its turn, probably gave rise to *Rhyacosiredon*. The Ambystomatinae can be divided into two subgroups: a plesiomorphic section including the *A. macrodactylum*, *A. maculatum*, *A. opacum*, and *A. cingulatum* species groups, and an apomorphic section including the *A. tigrinum* species group and the genus *Rhyacosiredon*. This makes continued utilization of subgenera of *Ambystoma* unnecessary. Continued recognition of *Rhyacosiredon* follows from the principles of evolutionary taxonomy (explicitly rejecting the contentions of cladism) and from Darwin's (1859) principles of classification (see above). Hypothesized cladistic relationships are shown in Figure 99 and the classification chosen to reflect this is given in Table 1.

It may seem in some ways more reasonable to split the Ambystomatinae into two genera according to the division into plesiomorphic and apomorphic sections. The structural differences between the two units are relatively distinct and such a move would reflect cladistic and patristic relationships. Nevertheless, this would lead to numerous nomenclatorial problems. The genus *Ambystoma* is based on the species *A. maculatum*, which would necessitate naming the more primitive section *Ambystoma*. With the suppression of the generic names senior to *Ambystoma*, it would seem that the first available name for the apomorphic section would be *Axolotes* Owen 1844 (see Tihen 1969, p. 75.1), with the type species as *Axolotes mexicanum* (= *Ambystoma mexicanum*). Inclusion of *Rhyacosiredon* in this genus would be problematical. Such a major change would engender extreme confusion and it is doubtful that it would be accepted. In order to promote stability, it is best that the nomenclature remain as it is.

It is accepted that ambystomatids are derived from hynobiid or pro-hynobiid stock (Tihen 1958, Larsen 1963, Regal 1966) and closely related to, or representative of, the actual ancestry of the Plethodontidae (Laurent 1947, Monath 1965, Regal 1966, Wake 1966). Ambystomatids share a common kind of trunk musculature with the Hynobiidae and are osteologically derivable from such ancestors. As argued above, they are related to the Amphiumidae and Scapherpetontidae, with which they are to be classified in the superfamily Ambystomatoidea. Basically on cranial evidence, close relationship of ambystomatids to plethodontids is well established (Regal 1966, Wake 1966). The character states shared by the two families are, however, basically of a primitive nature and, as argued below, I prefer to classify the Plethodontidae in their own suborder as they differ fundamentally in the structure of the trunk musculature.

Regal (1966) argued that *Rhyacotriton* could serve as a structural ancestor for the plethodontids, an hypothesis that finds support in the structure of the trunk musculature. *Rhyacotriton* has a simple, non-segmented *transversus* extending into the *subvertebralis*. Younger individuals of *Rhyacotriton* seem to lack the internal band of muscle fibers that extend anteromedially from the anterior basapophyseal septum. In older, larger individuals this layer is present. The smaller specimens have a condition very close to that of *Plethodon* and are structurally intermediate between the anterior basapophyseal and the posterior basapophyseal *subvertebralis*. In addition, the overlap of the *o. e. profundus* by a flap of the *rectus abdominis* resembles the plethodontid condition (compare Figs. 35 and 49). These resemblances, and the similarities of the auditory apparatuses (Larsen 1963, Monath 1965), are suggestive clues as to the origin of the Plethodontidae.

vii) Plethodontidae Gray 1850

CONTENT. *Plethodon* group: *Plethodon* Tschudi 1838, *Ensatina* Gray 1850, *Hemidactylium* Tschudi 1838, *Aneides* Baird 1849, ?*Batrachoseps* Bonaparte 1839; *Bolitoglossa* group: *Hydromantes* Gistel 1848, *Bolitoglossa* Duméril, Bibron, and Duméril 1854, *Lineatriton* Tanner 1950, *Thorius* Cope 1869, *Pseudoeurycea* Taylor 1944, *Chiropterotriton* Taylor 1944, *Oedipina* Keferstein 1868, *Parvimolge* Taylor 1941; *Eurycea* group: *Eurycea* Rafinesque 1822, *Gyrinophilus* Cope 1869, *Pseudotriton* Tschudi 1838, *Stereochilus* Cope 1869, *Haideotriton* Carr 1939, *Typhlotriton* Stejneger 1892, *Typhlomolge* Stejneger 1896; *Desmognathus* group: *Desmognathus* Baird 1850, *Leurognathus* Moore 1899, *Phaeognathus* Highton 1961.

FOSSIL RECORD. The record of plethodontids is sparse, consisting of a few trackways and several Pleistocene occurrences having little information on origins or intrafamilial relationships. Tihen (1968, p. 114) claims that fossils of *Plethodon* probably appear "before or during the Miocene," but the source of this is unknown to me. Peabody (1959) described lower Pliocene trackways from California referable to *Batrachoseps*, and Brame and Murray (1968) claimed these to belong to the extant *Batrachoseps relictus*. Vertebrae assigned to *Desmognathus* from the Pleistocene of Virginia (Gehlback 1965), *Plethodon glutinosus* from the Pleistocene of Florida (Holman 1958, 1959a,b), and *Pseudotriton ruber* from the Pleistocene of Georgia (Holman 1967) are also known.

RELATIONSHIPS. The phylogeny and classification of plethodontids have been a matter of dispute, although the situation has recently stabilized (Wake 1966). Unfortunately, the new information gained in this study and reinterpretation of previous data indicate the need for revision.

The first (and unsurpassed) detailed study of plethodontids, Dunn's (1926) *Salamanders of the Family Plethodontidae*, has had a lasting influence on concepts of relationship and it is now necessary to return to certain of Dunn's ideas. According to Dunn, plethodontids were derivable from salamandrids, except as regards the auditory apparatus. One of the major characters held to document the plethodontid-salamandrid relationship was the common occurrence of longitudinal rows of teeth along the palate. Noble (1931) noted resemblance between the "body musculature" of *Salamandra* and plethodontids, which has been confirmed by my study. However, Laurent (1947) demonstrated the basic dissimilarity of the vomerine and palatal teeth of plethodontids and the vomerine teeth of salamandrids. This evidence was accepted as justifying a change in classification, and plethodontids are now grouped with ambystomatids by most workers (Regal 1966, Wake 1966). This classification is based on features that are primitive for the Plethodontidae, but derived for the Ambystomatidae.

Regal (1966) suggested that *Rhyacotriton* is an acceptable structural ancestor for the plethodontids, as evidenced by the trunk musculature (discussed above) and similarities in development of the auditory structures (see Larsen 1963). Of course, certain autapomorphies prohibit the use of *Rhyacotriton* itself as a structural ancestor (i.e., loss of the nasal, loss of the *r. a. profundus*, chromosomal number of n=13).

The evidence from my study (see above), as well as data provided previously (Tihen 1958, Larsen 1963, Regal 1966, Wake 1966), indicates derivation of the Plethodontidae from a primitive ambystomatid or pro-ambystomatid. Shared similarities include: internal fertilization by means of a spermatophore, general configuration of the cranium, transverse vomerine tooth series (secondarily modified in plethodontids), patterns of the exits of spinal nerves (Edwards 1976), and general structure of the trunk musculature. Nevertheless, as argued under the Salamandridae below, I believe other information indicates that plethodontids should not be classified with the Ambystomatidae, but closer to the Salamandridae, with which they share basic adaptive trends. This is a return to the concepts of Dunn (1926) and Noble (1931), but for differing reasons and with differing details. It does not greatly affect the views of Regal (1966) and Wake (1966), but places different weights on certain characters.

Relationships within the Plethodontidae were first studied by Dunn (1926), who greatly influenced concepts of intergeneric relations up to the present. The work of Dunn was extremely detailed and well-reasoned, and I will argue for a return to certain of his ideas below. Since this time (Wilder and Dunn 1920, Dunn 1926) it has been accepted that plethodontids originated from ancestors inhabiting the mountain streams of Appalachia and reproducing aquatically (but see Salthe 1965, 1967, and below).

Dunn (1926) divided the Plethodontidae into desmognathines (*Desmognathus* and *Leurognathus*) and plethodontines as is presently accepted (Wake 1966), although without formal ranking. He separated plethodontines into two generic groups (on the basis of the condition of the tongue): the *Plethodon* group having a fixed-tongue (*Plethodon*, *Ensatina*, *Hemidactylium*, *Aneides*, and *Batrachoseps*) and the free-tongued *Eurycea* group (*Eurycea*, *Gyrinophilus*, *Pseudotriton*, *Stereochilus*, *Typhlotriton*, *Typhlomolge*, *Hydromantes*, and "*Oedipus*"). *Gyrinophilus* was judged the most primitive living plethodontid, but he stated that *Plethodon* was also very primitive and derivable from no living genus.

In a phylogenetic reconstruction quite similar to that proposed below, Piatt (1935, p. 238, figure not numbered) suggested that the free-tongued species were diphyletic. "*Oedipus*" (= the supergenus *Bolitoglossa* of Wake 1966) and *Hydromantes* were judged to have been derived from an ancestor in common with the *Plethodon* group, while *Eurycea* and its allies were earlier independent derivatives. Piatt did not consider *Batrachoseps* to be as close to *Plethodon* as had Dunn.

By contrast, Tanner (1952), also basing his conclusions primarily on data from the hyobranchium and its associated musculature, united the free-tongued plethodontids as a monophyletic group. Wake's (1966) phylogeny of the Bolitoglossini is almost identical to that of Tanner, differing as regards the relationships of *Thorius* and *Hydromantes*. Wake removed *Hemidactylium* and *Batrachoseps* from Dunn's *Plethodon* group, placing them in the *Eurycea* group (renamed the Hemidactyliini) and with the neotropical free-tongued plethodontids (the Bolitoglossini), respectively. He considered *Hemidactylium* to be the most primitive living plethodontid, a conclusion controverted by my findings. Wake's (1966) phylogenetic reconstruction has the Hemidactyliini as the central plethodontid stock, with the Desmognathinae, Bolitoglossini, and Plethodontini branching sequentially from it.

More recently, Wake and Lombard (1973, p. 65) implicitly question this scheme, stating that "direct development only [evolved] once." This might seem to indicate that they consider bolitoglossines to have evolved from the Plethodontini, although later interpretations seem not in agreement (Lombard and Wake 1976).

I suggest a return to the basic concepts of Dunn (1926) and Piatt (1935), my classification being shown in Table 2. These changes from Wake's (1966) groupings involve taking *Hemidactylium* from the Hemidactyliini (to be called the Euryciini) and *Batrachoseps* from the Bolitoglossini, and placing them in the *Plethodon* group (tribe Plethodontini). My scheme differs from that of Dunn in considering the free tongue to have evolved twice.

Formal classification reflecting phylogeny (see Fig. 100, and below) necessitates recognition of two subfamilies: the Plethodontinae, with the tribes Plethodontini and Bolitoglossini; and the Desmognathinae, with the tribes Euryciini and Desmognathini. I am somewhat hesitant to suggest this step owing to the use of the subfamily Desmognathinae to contain only *Desmognathus* and its allies. Nevertheless, these formal groupings will be used here as they and the proposed phylogeny are in agreement with my studies on the trunk musculature, consistent with cranial osteology, more parsimonious with respect to biogeography, and (if the reinterpretation is accepted) consistent with life history data.

In terms of cranial anatomy, *Plethodon* is one of the most primitive of living plethodontids. Although Wake (1966) believed *Gyrinophilus* to be more primitive, my interpretation of his data and of the crania indicates that they are probably equally primitive in this regard. The structural primitiveness of *Plethodon* is even more pronounced in the trunk musculature and hyobranchium (see Wake 1966, Piatt 1935, and above). The axial musculature of *Plethodon* is an almost perfect structural intermediate between the anterior basapophyseal musculature of primitive salamanders and the posterior basapophyseal sort of more derived plethodontids. In all apparent aspects, *Plethodon* is structurally ancestral to other plethodontids.

As noted by Dunn (1926), and corroborated by Wake (1966), *Ensatina* and *Aneides* are osteologically derivable from *Plethodon*. The detailed structure of the trunk musculature confirms this. The position of *Hemidactylium* has been uncertain: earlier workers (Dunn 1926, Noble 1931, Piatt 1935) derived it from *Plethodon*, but Wake (1966) indicated a closer alliance with the *Eurycea* group. Dunn (1926, p. 25) stated that *Hemidactylium* "has reverted to some extent to the still water breeding site of more primitive salamanders," and Noble (1931) supported this. Although Wake (1966) disagreed, believing the aquatic larval stage of *Hemidactylium* to be primitive, he provided no evidence to controvert Dunn's suggestions.

The eggs of *Hemidactylium* are laid amongst sphagnum moss along the edges of ponds, where they are attended by the female. Upon hatching, the young wriggle into the water where a short period (about six weeks) is spent prior to metamorphosis (Dunn 1926, Bishop 1943). The adult is terrestrial and avoids water. The filamentous gills of larval *Hemidactylium*, the possession of only three branchial bars, the position of egg deposition and the brooding female, the short larval period, and the close structural resemblances between adult *Plethodon* and *Hemidactylium* all indicate the secondary nature of the latter's reproductive strategy. Lombard and Wake (1977) have shown resemblances in the tongue of *Hemidactylium* to that of *Plethodon* and its allies. Notably, the *genioglossus* of *Hemidactylium* is very like that of *Ensatina*, but differs from that of *Eurycea* and its relatives. The tongue of *Hemidactylium* is fixed as in all members of the *Plethodon* group, but unlike terrestrial euryciines. This reinterpretation does little violence to Wake's (1966) reconstruction, in which he noted that *Hemidactylium* was the most isolated "hemidactyliine." The genus fits much more readily into the Plethodontini.

The relationships of the bolitoglossines and of *Batrachoseps* have been uncertain. Dunn (1926) believed the free-tongued forms to be a natural group, as did Tanner (1952). Piatt (1935), however, argued that *Hydromantes* and "*Oedipus*" were not closely related to the eastern free-tongued plethodontids, but from *Plethodon* stock. Regarding the position of *Batrachoseps*, Dunn (1926), Noble (1931), and Tanner (1952) placed it with the *Plethodon* group (the Plethodontini), whereas Piatt (1935) argued that it was related to the bolitoglossines.

Wake (1966) separated *Hydromantes*, the supergenus *Bolitoglossa* (= "*Oedipus*" of the older workers), and *Batrachoseps* into the tribe Bolitoglossini, believing the latter to have originated from the Euryciini (his Hemidactyliini). Based on my studies and on reinterpretation of data previously published, however, the more reasonable interpretation is that the free tongue is diphyletic: the bolitoglossines being of *Plethodon* origin and distant from the eurycines.

If Wake's (1966) phylogenetic reconstruction of the tribes Hemidactyliini, Plethodontini, and Bolitoglossini is accepted, monophyletic origin of the free tongue is difficult to support. Deriving the latter two tribes independently from "hemidactyliines" presents only two possibilities: 1) the free tongue is monophyletic, indicating that the attached tongue in the Plethodontini is secondary, a most unlikely interpretation, or 2) the free tongue is diphyletic, the fixed tongue being primitive in the Plethodontini. The latter interpretation is the only reasonable one in Wake's context (as well as my own), especially considering the structure of the hyobranchial apparatus in *Plethodon* and its allies (see Lombard and Wake 1976, 1977). Except for common possession of the free tongue, bolitoglossines and euryciines share no characters indicating close relationship.

The *subvertebralis* of *Bolitoglossa* shows posterior flexures that are not intimately associated with the posterior basapophyseal regions of the vertebrae (contrast euryciines). *Hydromantes* has this flexure associated more closely with the transverse process. *Pseudoeurycea* has the posterior flexure extending beyond the posterior basapophyseal region. *Chiropterotriton* has species in which the *subvertebralis* is similar to that of *Bolitoglossa*, whereas other species lack all trace of posterior flexures, the subvertebral fibers being limited to passing between two adjacent vertebrae and ribs (compare Figs. 58, 59, and 60).

The trunk musculature of the supergenus *Bolitoglossa* and of *Hydromantes* is more readily derivable from the system of *Plethodon*, although admittedly evidence from a single character complex cannot provide definitive data against a connection with the Euryciini.

The cranium (see Wake 1966) is derivable from that of *Plethodon*, as is the throat musculature and hyobranchium (see Piatt 1935, Tanner 1952, Lombard and Wake 1976, 1977). Such a derivation is more parsimonious than Wake's (1966) proposal in that it does not call for hypothetical wanderings of taxa westward, but is consistent with known present distributions. Lombard and Wake (1977) have documented fundamental dissimilarity in the structures and mechanisms of protraction of the hyobranchium between the eastern and western free-tongued plethodontids, further corroborating the relationship between plethodontines and bolitoglossines.

The relationships of *Batrachoseps* are obscure, but I believe it to be most closely related to the Plethodontini (see Dunn 1926, Tanner 1952). Certainly no persuasive evidence against Dunn's original grouping has been proposed. If, as suggested by Wake (1966), *Batrachoseps* is closer to the supergenus *Bolitoglossa* than either of these is to *Hydromantes*, there are only two possibilities regarding the free tongue of the Bolitoglossini: 1) *Batrachoseps* has secondarily lost the free tongue, or 2) the free tongues of *Hydromantes* and of the supergenus *Bolitoglossa* are of separate origins.

The first possibility is unlikely and without any supporting evidence. The second possibility is also probably not true (although see Lombard and Wake 1977), making it necessary to reject close affinity of *Batrachoseps* and *Bolitoglossa*.

If the bolitoglossines are a monophyletic group, *Batrachoseps* must be more primitive than any of the former's living representatives. This means that it would be the plesiomorphic sister-group of

Hydromantes plus the supergenus *Bolitoglossa*. The evidence is not definitive (and *Batrachoseps* does share resemblances with the bolitoglossines, see Wake 1966), but I prefer to classify *Batrachoseps* within the Plethodontini. Although at least one species of *Batrachoseps* (*B. attenuatus*) has simplified subvertebral myomeres, as do at least some bolitoglossines (*Chiropterotriton chiroptera*), the distribution of this feature shows it to be all but certainly owing to convergence.

The Plethodontinae are, therefore, composed of two tribes, of which the Plethodontini are the most primitive and the Bolitoglossini are derived from it. The other plethodontid subfamily, the Desmognathinae, is probably derived from ancestry in common with the Plethodontinae and also composed of two tribes. With the removal of *Hemidactylium*, the Euryciini appear to be a natural group (see above descriptions, and data in Wake 1966, Lombard and Wake 1977). Within this group, both Dunn (1926)and Wake (1966) considered *Gyrinophilus* to be the most primitive. As regards cranial osteology, this seems true, but the structure of the trunk musculature creates complications. *Eurycea*, in some respects, perhaps presents a more primitive development of the axial musculature. That is, there is less accentuation of the posterior basapophyseal system and less emphasis of vertebral processes and crests (although these features may be secondary).

My theory of the relationships of the Plethodontini and Euryciini follows basically from the following morphocline in the structure of the trunk musculature:

Plethodon — *Hemidactylium* — *Eurycea* — *Gyrinophilus* — *Pseudotriton*.
This cline is not, however, claimed to be a phylogenetic sequence.

Hemidactylium is in many respects a structural ancestor for the Euryciini, as recognized by Wake (1966). A morphocline based on the cranium, for example, would be somewhat different, but probably the major obstacle to acceptance of the plethodontines as primitive with respect to the euryciines is the present belief that aquatic larvae are primitive to the Plethodontidae. There are indications that aquatic reproduction may be a secondary phenomenon, however.

Except for desmognathines, plethodontids possess only three branchial arches as embryos, larvae or both (see Piatt 1935, Dunn 1926). This could be taken as indicating reduction during an ancestral stage in which all plethodontids underwent direct development. Furthermore, the external gills of the larvae tend to be filamentous, as in the embryos of the genus *Plethodon*, rather than of the primitive form seen in hynobiids, ambystomatids, and even salamandrids (see Noble 1931, Bishop 1943).

The auditory apparatus of plethodontids seems to be basically an adaptation for terrestrial life (see Larsen 1963, Monath 1965, Reed 1920). The trunk musculature of *Plethodon* is unarguably more primitive than that of any member of the Euryciini or Desmognathini, while its cranial structure is at least equally primitive. The criterion of correlation of characters would indicate, although very tentatively, that perhaps the pattern of breeding is equally primitive.

Salthe (1967) shows that, where known, the courtship patterns of plethodontids are basically of a terrestrial sort. That is, the female is attracted to the dorsal region of the male's tail during spermatophore deposition, not to the cloaca as in ambystomatids and salamandrids (which breed aquatically). In water, cloacal secretions generally provide the attractant. Salthe (1965) has argued for the terrestrial origin of plethodontids, based on the occurrence of lunglessness throughout the family.

The adaptation of the female brooding her clutch, whether on land or in water, is present throughout the family. All members of the Plethodontini have brooding, except for at least some species of *Batrachoseps* and this is probably a secondary adaptation to arid environments (Maiorana 1976, Dunn 1926, Bishop 1943). Bolitoglossines are probably all brooders, as are *Desmognathus*, *Leurognathus*, and almost certainly *Phaeognathus*, which is a terrestrial burrower (Dunn 1926, Martof 1962). Data on members of the Euryciini are less extensive. At least some *Gyrinophilus*, *Pseudotriton*, *Stereochilus*, and some *Eurycea* brood the young and it would seem probable that others have the same reproductive strategy (see Bishop 1943, Salthe and Mecham 1974). This kind of reproduction would probably most readily evolve in a terrestrial situation.

Desmognathus and *Leurognathus* have been extensively studied in terms of structure (Wake 1966, Dunn 1917, above descriptions) and life history (Dunn 1917, Organ 1961, Martof and Scott 1957, Martof 1962). Dunn (1917, 1926) and Organ (1961) noted the following relationships of the species of the two genera:

FOREST	*D. carolinensis* — *D. ochrophaeus*
BROOK	*D. monticola* — *D. fuscus* — *D. auriculatus* — *D. brimleyorum*
STREAM	*D. quadramaculatus*
AQUATIC	*Leurognathus marmoratus*

Moving both from bottom to top and left to right on the chart there is an increase in terrestrialism, with a decrease in the length of the aquatic larval stage until it disappears. It has been assumed that those species having aquatic larvae are the most primitive in the group and that an evolutionary trend to increasing terrestrialism is being reflected. However, it is perhaps not unreasonable to ask whether there might not be another interpretation. The *Desmognathus* group is highly derived, with numerous apomorphic character states in the cranium (Wake 1966) and trunk region (see above). Structurally there is no reason to assume the Desmognathini to be an early offshoot from plethodontid stock. Rather, they are most readily derivable from the structural plan exhibited by the Euryciini, being the culmination of the trends exhibited by the latter. Only the breeding pattern would indicate early derivation.

The reproductive pattern of *Desmognathus fuscus* is well understood and sheds light on the question of the primitive nature of aquatic reproduction. "The eggs are guarded by the mother [on land] . . . . The period from laying to hatching is about five weeks. When hatched the larvae measure 15 mm. There is a terrestrial larval stage of 15 to 16 days. At the expiration of this period the length is about 20 mm. and the larvae enter the water" (Dunn 1917, p. 411). This increase in size during the terrestrial phase may indicate that food is taken. Noble (1931, p. 56) noted that "the young Dusky Salamander [*D. fuscus*], during the first two weeks of its life, is not merely a larva which chances to be hatched at a distance from its aquatic habitat, but it is a terrestrial salamander fully able to move about in the damp cracks and crannies leading from the nest to the nearest pool." The tail fin and gills, which lack distinct central rami and are somewhat filamentous, develop only upon the larva's entering the water.

Wilder (1917, p. 17) stated: "That the terrestrial larval stage [of *D. fuscus*] is really a definite one is shown by the behavior of the newly hatched larvae when placed in water . . . they will not remain in the water, but persistently crawl out . . . . It is not until all external evidence of the yolk mass has disappeared that they will remain in the water." Noble and Evans (1932, p. 8) "found that *Desmognathus fuscus fuscus* was able to pass through its larval stage on land without having access to free water," but that it was also possible to force them to become aquatic immediately upon hatching. This indicates plasticity in development. These facts intimate that the aquatic "larval" phase has perhaps been secondarily added to the life-cycle and that those members of the Desmognathini that lay aquatic eggs may do so secondarily.

Rather than interpreting the sequence as stream to stream-bank to forest as diagrammed above, it is equally possible that the desmognathine sequence is forest to stream-bank, or stream-bank to both forest and stream. If either of the latter is true, then justification for continued recognition of the genus *Leurognathus* is slight. Under this new view, *Leurognathus* fits well into the morphocline of the genus *Desmognathus*.

In spite of the various facts tending to support the theory, there are certain problems with its acceptance. These include:

retention of a coronoid in larvae of some plethodontids, the four branchial arches of larval desmognathines (as opposed to three in other plethodontids), and the coherent theory of the mountain-brook origin of the lungless condition. These urge caution in the evaluation of the hypothesis here proposed, and there are several alternative possibilities:

1. The aquatic larvae of the Euryciini and Desmognathini are primitive, as suggested by previous workers. This would indicate a sister-group relationship between the Plethodontinae (terrestrial eggs) and the Desmognathinae (aquatic larvae), with each unit retaining certain primitive features and having developed other, apomorphic ones.

2. The aquatic larva of all plethodontids is secondarily derived, the reproductive pattern of the Plethodontini and Bolitoglossini being primitive.

3. Various combinations of alternative two: perhaps the Euryciini are secondarily aquatic and the Desmognathini primarily so, or vice versa.

At present, although I would urge careful consideration of the second possibility, the first alternative is probably the most reasonable.

The Plethodontidae are, therefore, to be divided into two subfamilies sharing a sister-group relationship. The Plethodontinae consist of two tribes, the Plethodontini and the Bolitoglossini, which are united on the basis of reproductive patterns, axial musculature, and basic osteology. The Desmognathinae are also comprised of two tribes, the Euryciini and the Desmognathini, which share a common sort of reproduction, the same basic plan of trunk musculature, similar osteology, and inhabit a common geographical area. What I believe to be the phylogenetic relationships of these higher taxa is shown in Figure 100, and the classification is given in Table 2. It is not profitable to attempt a lower-order phylogenetic reconstruction of the Plethodontidae. Any sort of generic phylogeny can be little more than more or less untestable guesses in this family.

Although, at first sight, it may appear that my phylogenetic reconstruction (Fig. 100) and classification (Table 2) disagree to a major extent with those of Wake (1966), such is not the case. Wake (1966) recognized the primitive nature of *Hemidactylium* within his tribe Hemidactyliini. I agree that it is probably related to *Eurycea*, but also that it is related to the *Plethodon* group. As its trunk musculature, lack of a free tongue, and secondary return to aquatic reproduction (Dunn 1926) all differ from members of the Euryciini, and as it shares features that are derived with respect to the Plethodontini, but primitive with respect to the Euryciini, it fits better with the former tribe. Wake (1966) also recognized the relationship of the Desmognathini to the Euryciini. My scheme simply indicates a closer relationship, as anticipated by Noble (1927). The major difference in our interpretations concerns the bolitoglossines, which I, in agreement with Piatt (1935), consider derived from the Plethodontini. This fits better with present geographic ranges, anatomical evidence (hyobranchial, osteological, and axial), and breeding data than the theory of Wake (1966).

The Plethodontidae are closely related to both the Ambystomatidae and to the Salamandridae. As argued below, I consider the family to be best grouped with the families having posterior basapophyseal musculature, as this reflects a basic adaptive shift and allows splitting of the Caudata into two subequal suborders.

viii) Proteidae Hogg 1838

CONTENT. *Proteus* Laurenti 1768, *Necturus* Rafinesque 1819, ?*Orthophyia* von Meyer 1845, ?*Hylaeobatrachus* Dollo 1884.

FOSSIL RECORD. The fossil record of proteids is spotty and of uncertain interpretation. *Comonecturoides marshi*, represented by a single right femur from the Upper Jurassic of Wyoming, was referred to the "Necturidae" by Hecht and Estes (1960), but the proper classification of this monotypic genus is uncertain. Herre (1935b) described *Palaeoproteus* from the Eocene of Europe as a primitive proteid, but Estes et al. (1967) referred it questionably to the Salamandridae. Arguments for classifying it with the Batrachosauroididae are presented below.

Hylaeobatrachus croyi Dollo 1884 from the Lower Cretaceous of Belgium is also of uncertain relationship. Although Wiedersheim (in Dollo 1884) considered it to be a salamandrid, it is usually referred to the Proteidae (see Kuhn 1962). If truly a Proteid, it is very primitive: there are only 17 presacral vertebrae, there are four toes on the front and five on the hindlimbs, and well-developed maxillae are present (see Kuhn 1962, Dollo 1884, figs. 1 and 2). On the other hand, it is definitely paedogenic, with external gills and three ossified branchial arches. Although the type specimen has been lost, Estes is presently studying the counterpart.

Vertebrae of *Necturus* from the upper Paleocene Ravenscrag Formation of Saskatchewan have recently been discovered (see Fig. 13) and are described elsewhere (Naylor 1978b). *Necturus* is questionably known from the Oligocene of North America (Romer 1966, Estes pers. comm.). Lynch (1965) reported vertebrae of *Necturus* from Florida, which are somewhat outside the present range of the genus.

Two species of *Orthophyia* have been named from the Miocene of Switzerland (von Meyer 1845). This genus is usually referred to the Proteidae (Brame 1967, Kuhn 1962), but all known material has been lost. Estes and Darevsky (1977) name a new genus and species of Proteid, *Mioproteus caucasicus*, from the Miocene of the Caucasus, which they suggest might be the same as *Orthophyia*. *Mioproteus* has relatively robust vertebrae with distinct posterior basapophyses and a ring of calcified tissue within the anterior cotyle. It shows resemblances to batrachosauroidids, as well as to *Necturus* and (especially) *Proteus*. *Proteus bavaricus* is based on a parasphenoid from fissure fillings of Pleistocene age in Germany (Brunner 1956), but as noted by Estes and Darevsky (1977) the figure and description of this material are inadequate.

The known fossils contribute little to understanding of the relationships of the Proteidae, but further study of known specimens might well produce valuable information.

RELATIONSHIPS. Before discussing the relationships of proteids to other salamanders, it is necessary to consider the kinship of *Necturus* and *Proteus*. Following an earlier argument of Hecht's (1957), Hecht and Edwards (1976) attempted to demonstrate that *Proteus* and *Necturus* are not especially related. Although characters are rejected as having no phylogenetic information owing to their being loss characters, presumably primitive, or paedogenic, no positive data are presented in support of the thesis. Positive evidence for monophyly has been presented in various papers. Kezer and his co-workers have provided strong karyological evidence of the close relationship of proteids (Kezer, Seto, and Pomerat 1965, Leon and Kezer 1974). Larson and Guthrie (1974) present data from the skull, auditory region, and hyobranchium that are in support of a theory of monophyly. Study of the trunk musculature (see above) and of spinal nerve exits (Edwards 1976) indicate relationship. Indeed, taken together, the characters listed by Hecht and Edwards (1976) demonstrate the probability of monophyly.

There is often a tendency to use paedogenesis or neoteny to exclude characters from consideration and to "explain" the existence of features. Paedogenesis and neoteny are not equivalent phenomena as regards their expressions in the different families of salamanders. Although owing to the retention of larval features in breeding adults, the expression of paedomorphosis is highly variable. Hynobiids, ambystomatids, plethodontids, and salamandrids all have neotenic (facultatively metamorphosing) representatives, but none could be confused with those of another family. Cryptobranchids, amphiumids, proteids, sirenids, and some plethodontids are, to a greater or lesser degree, paedogenic. Nonetheless, each family is distinct structurally and ecologically, and if fossil forms are considered, the Scapherpetontidae and Batrachosauroididae are also distinctive paedogenes. The important point is that, within the adaptational strategy termed paedogenesis, there is a wide variety of distinctive structural plans and *Necturus* and *Proteus* share one of these. Owing to differences in ancestry and consequent selection, distinctive structural changes have taken place in each family. This is especially important in view of the fact that *Necturus* and *Proteus* have quite different ecological relationships, indicating that the similarities are owing to descent.

It is invalid, therefore, to dismiss characters uniquely shared between *Proteus* and *Necturus* as paedogenic or primitive, thereby implying that they mean nothing. Whereas one or two such characters could be so treated, fourteen such characters cannot be rejected. In total, the character states shared by proteids serve to clearly distinguish them from all other paedogenic and neotenic urodeles and, at the same time, provide overwhelming evidence for monophyly.

The features considered by Hecht and Edwards (1976) include:

1. *The perennibranchiate condition.* This differs from aphiumids and cryptobranchids, and the gills differ structurally from those of other perennibranchiates.

2. *Presence of two gill slits.* Although paedogenic, this feature is unique amongst "larval" salamanders.

3. *Proportions of the skull.* Again, although in a limited sense "paedogenic," these proportions are unique to the Proteidae.

4. *Absence of maxillae, septomaxillae, lacrimals, nasals, and prefrontals.* These features are treated as having no taxonomic

information owing to their being "loss characters." Nevertheless, although perhaps of minor importance, such losses do provide some phylogenetic information, especially when taken together and in combination with other data. The loss of all these bones is unique to the Proteidae, indicating monophyly.

5. *Broad parasphenoid.* Certainly a "larval" condition, but, as noted by Estes (1975, p. 372), its "close approximation to the condyles is unusual," and the overall shape is also unique.

6. *Separate opisthotic.* This unique character was rejected as having no information content owing to its presumed paedogenic nature. Hecht and Edwards (1976) note that certain larval salamanders show three separate regions of ossification in the otic region. Cloete (1961), although cited by these workers, makes no mention of a separate opisthotic centre of ossification in *Rhyacotriton* that I can find. Bonebrake and Brandon (1971, pp. 199-200) state that "the ossifying opisthotic expands over the posterior surface of the otic capsule in stage VI [and] it reaches and fuses indistinguishably with the dorsal process of the exoccipital" in *Ambystoma texanum*. Parker (1878, cited in Bonebrake and Brandon 1971) described a separate opisthotic in *Ambystoma mexicanum* (as *Siredon*) and *Siren*.

Although it is, therefore, true that the presence of the opisthotic *per se* may not represent a shared-derived character in proteids, this does not settle the question. The opisthotic is retained in both *Necturus* and *Proteus* as a separate element in the adult, not merely as a transitory stage. It is expanded in the same way and distinctly altered to the same shape in both genera. This common character is thus almost certainly a shared-derived character, indicative of close genealogical relationship.

7. *Non-pedicellate teeth.* This feature is larval, but the development is similar in each genus, with a zone of weakness (see Means 1972, Larsen and Guthrie 1974).

8. *Hyobranchium.* The similarities are dismissed as "larval" and "primitive." First of all, the hyobranchium is all but certainly not primitive, but highly apomorphic (compare that of hynobiids, Edgeworth 1923). Secondly, although the resemblances are, to a certain extent, owing to paedogenesis, they are also derived. That is, the hyobranchium of each genus is more similar to that of the other than to that of any other "larval" salamander (see Larsen and Guthrie 1974, Cope 1889).

9. *Chromosome data.* These are dismissed as not "certain evidence of monophyly" (Hecht and Edwards 1976, p. 666), but the common possession of a chromosome number of n=19, and close similarities in the structures of individual chromosomes between the genera do provide positive and important support (not, of course, proof or "certain evidence") for an hypothesis of monophyly (see data in Kezer et al. 1965, Morescalchi 1975). It is possible that the number of n=19 and the similar structures developed convergently, but this is certainly less likely (especially in light of the other anatomical evidences) and unparsimonious. References to ultimately non-explanatory concepts of "karyotypic orthoselection" are not sufficient to explain away these similarities.

10. *Pattern of spinal nerve exits.* This shared character state is dismissed as "primitive" and, therefore, not to be "considered

evidence for monophyly or phyletic affinity" (Hecht and Edwards 1976, p. 664). However, shared characters, even though judged primitive by a researcher, do hold information as to the relationships of taxa. The spinal nerve data are also of interest in light of the structure of the axial musculature of proteids. Both genera have closely similar patterns in the *dorsalis trunci*, *subvertebralis*, and lateral abdominal musculature. These patterns are consistent only with derivation of *Proteus* and *Necturus* from an ancestor having opisthocoelous or proto-opisthocoelous vertebrae (that is, from a relatively derived ancestor). It is, therefore, likely that the complete lack of intravertebral postatlantal exits for spinal nerves is a secondary phenomenon (only cryptobranchoids and batrachosauroidids have this pattern amongst other salamanders). If this interpretation is true, then the common lack of spinal nerve exits except through the atlas is a shared and derived character.

11. *Loss of the fourth branchial arch.* Owing to its nature (a loss character), this feature cannot be given major taxonomic weight, but in combination with the other features it is another positive evidence.

12. *Distribution of the palatal teeth.* This is rejected as a "larval" condition, which is (in a very limited sense, compare hynobiids and ambystomatids) true. Nevertheless, and more to the point, this condition clearly distinguishes both *Proteus* and *Necturus* from other paedogenic salamanders. The distribution of the palatal teeth is to be regarded as a shared and derived character, which has evolved via paedomorphosis.

13. *Absence of ypsiloid cartilage.* This feature is claimed to be of low taxonomic importance in that it is a loss character. This is true to the extent that the ypsiloid has been lost convergently in several other groups (e.g., amphiumids and plethodontids), but the common presence of the anterior cartilaginous projection from the pubis in *Necturus* and *Proteus* is an apomorphic character.

It is not sufficient to state that "the form of the sacral projections was different in the two genera, implying that they developed independently" (Hecht and Edwards 1976, p. 664), nor does Hecht's (1957) claim that it is a "neotenic adaptation" explain away the structure. Other paedogenic or neotenic urodeles lack all trace of an anterior projection from the pubis. *Cryptobranchus*, which is elongated to much the same extent as *Necturus* and also paedogenic, lacks the projection and retains the ypsiloid. In *Amphiuma* the ypsiloid is lacking, but no projection develops. In larvae and neotenes of other families a fully functional ypsiloid is usually present. If absent, as in plethodontids, no special projection develops.

The absence of the ypsiloid and its replacement by the triangular cartilage extending from the pubis is an apomorphic feature shared by the two genera and is another significant positive evidence for monophyly.

14. *Structure of the columella.* This feature is rejected by Hecht and Edwards as being of minimal importance owing to "heterotropic" origin and dependence on allometry. Once again the detailed similarity between *Proteus* and *Necturus* is overlooked and the common

lack of an operculum dismissed. Larsen and Guthrie (1974) have demonstrated detailed resemblance in the structure of this region between the two proteids. More or less vague resemblances to *Ambystoma mexicanum* cannot be validly used to cause rejection of this shared and derived character. Furthermore, the common development of a structure, whether owing to allometry or anything else, provides evidence potentially in support of genealogical relationship. Allometry and neoteny may well affect the development of certain structures, but such statements ultimately say little as to their apomorphic status.

If further evidence were required, data from my studies of the trunk musculature show close and detailed resemblance of the epaxial and hypaxial units. These resemblances are almost certainly characters derived from a common ancestor, and differ from those of all other paedogenic salamanders. Rejection of the similarities of the trunk musculature as paedogenic, primitive, allometric, or owing to orthoselection is not plausible.

It is to be concluded that the characters presented by Hecht and Edwards (1976) provide very good evidence for a theory of monophyly for *Proteus* and *Necturus*. Even if true that an argument can be made that any given character should, by itself, not be accorded major taxonomic weight, when the characters are considered together they are important and convincing. In systematics one treats entire organisms, not isolated characters. It is necessary to be concerned with what the characters altogether mean, not with mere descriptive discussion of them (i.e., that a feature is neotenic, paedogenic, owing to loss, primitive, or whatever). Characters judged to be in any of these categories often still carry important taxonomic and phylogenetic information. Proteids are, therefore, to be considered as most probably a monophyletic group, the polyphyletic hypothesis having been shown to be very unlikely (see also Kezer et al. 1965, Brandon 1969, Leon and Kezer 1974, Larsen and Guthrie 1974).

Knowledge of the relationships of the Proteidae to other salamanders has been uncertain. Cope (1889) suggested that proteids were very primitive and placed them in a separate order in a position ancestral to his order Urodela. Reed (1920), on the basis of the auditory apparatus, included them in a legion along with plethodontids and amphiumids. Dunn (1926) classified proteids in his Salamandroidea, along with the "higher" salamanders (ambystomatids, plethodontids, amphiumids, and salamandrids), but noted that they were "not obviously related to any one of the other families" (p. 3).

Noble (1931, p. 483), however, placed them in a separate suborder, stating that they "form a natural group . . . of unknown ancestry," but perhaps derived from salamandrids. He noted that the cloacal glands resemble those of amphiumids, salamandrids, and plethodontids. Herre (1935b), basing his conclusions on osteology and the Eocene *Palaeoproteus*, derived proteids from the salamandrid newts. Wake (1966) divided proteids into separate families (Necturidae and Proteidae), which he placed with salamandrids and amphiumids in the suborder Salamandroidea. Regal (1966) utilized only the single family Proteidae, placed alone in the Proteida.

Salthe (1967) suggested that what is known of the breeding of *Proteus* resembles that of *Triturus* and that courtship could be taken to indicate that proteids were diphyletic. As the courtship of *Necturus* is all but unknown, however, these data are not convincing. Primarily on the basis of karyology, Morescalchi (1973, 1975) derived proteids from ancestry close to that of the Sirenidae and in common with that of the "higher" salamanders (those families having internal fertilization). Leon and Kezer (1974), also on the basis of chromosomal data, suggested that proteids and salamandrids share a common ancestor. Most recently, Edwards (1976) produced a cladogram that shows proteids as the plesiomorphic sister-group of batrachosauroidids, amphiumids, plethodontids, ambystomatids, scapherpetontids, and salamandrids.

In spite of uncertainty regarding the affinities of the Proteidae, it is now possible to develop a well-based hypothesis of relationships. Estes (1975) suggested that the Batrachosauroididae are closely related to proteids. It will be argued that this hypothesis is the most reasonable in light of the fossil evidence, comparative osteology, and information from the trunk musculature. Estes noted resemblances between *Opisthotriton* and proteids in the structure of the squamosal (with a columellar process), the vomers and vomerine teeth, the broad posteriorly produced parasphenoid, structure of the teeth (non-pedicellate), "general aspect" of the hyobranchial skeleton, and the *Necturus*-like vertebrae of *Opisthotriton*. In addition to these, the following are also general resemblances between the two families: the structure and relationships of the vomers and palatines and of the associated teeth, the premaxillae with long and separate nasal spines, the small odontoid process of the atlas, and the caudal vertebrae with long, tubular hyperapophyses and haemal spines. These general and specific resemblances are very suggestive.

The relationship is further indicated by considerations of the trunk musculature in Recent proteids, the theory of the development of opisthocoely presented above, the new Miocene proteid discovered in the Caucasus (Estes and Darevsky 1977), and the spinal nerve data presented by Edwards (1976). Batrachosauroidids, having opisthocoelous vertebrae, could only have evolved from ancestors having posterior basapophyseal musculature (see above, also Figs. 94, 95, 96, and 97). *Opisthotriton* and *Prodesmodon* (as reinterpreted, Naylor 1978a) have well-developed posterior basapophyses, confirming the presence of such musculature. Opisthocoely also correlates, at least among living salamanders, with a general simplification of the *dorsalis trunci*.

With respect to proteids, which are fully amphicoelous, the structure of the trunk musculature indicates derivation from an opisthocoelous ancestor (compare descriptions of proteids, plethodontids, and cryptobranchids above). The *dorsalis trunci*, although massive, has a simplified myoseptal pattern, while the *subvertebralis* is very simple in comparison to that of cryptobranchoids and ambystomatoids, retaining only posterior flexures. Derivation of the proteid pattern of trunk musculature directly from the anterior basapophyseal sort without an intervening stage such as that represented by the Batrachosauroididae is unlikely. The newly discovered *Mioproteus* further supports this suggestion. The vertebrae possess posterior basapophyses and a ring of calcified tissue inside the anterior cotyle, the latter perhaps being a remnant of opisthocoely. *Mioproteus* thus shows resemblance to both batrachosauroidids and proteids (see Estes and Darevsky 1977 for figures and descriptions).

Proteids are also like batrachosauroidids in the pattern of the spinal nerve exits (see Edwards 1976) and the overall structure of the atlantes, with small or nonexistent odontoid processes. Further evidence of the suggested relationship can, perhaps, be gained from the following morphocline of vertebral structure (this does not purport to be a phylogenetic event, but probably is consistent with such a sequence):

Batrachosauroides — *Necturus*
Prodesmodon — *Opisthotriton* —
Palaeoproteus — *Proteus*

In this series (see Fig. 12, also Estes 1964, figs. 38, 41 and 42, 1969a, figs. 1, 3 and 5) is documented progressive reduction of the degree of opisthocoely and of basapophyses down to complete loss. This could well be the actual structural sequence involved in the evolution of proteids, but no ancestor-descendant relationships are claimed.

If close relationship between proteids and batrachosauroidids is accepted, they must be clasified together. I prefer to follow Estes (1975), who recognized two families in a single higher taxon, here the superfamily Proteoidea. The problem is now a resolution of the position of this superfamily within the Caudata.

Proteoids possess several characters forbidding close affinity with the Cryptobranchoidea: elongate premaxillary spines, fusion of angular and prearticular in the lower jar, and (at least in proteids) internal fertilization by means of a spermatophore. Distinction from the Ambystomatoidea is shown by the possession of opisthocoelous vertebrae or simplified, posterior basapophyseal musculature. On the basis of these features, the Proteoidea may be separated from the more primitive urodeles (the Cryptobranchoidea and Ambystomatoidea, see above) and united with plethodontids (the Plethodontoidea) and salamandrids and sirenids (the Salamandroidea, see below). Affinity to the latter superfamilies is also indicated by the reproductive patterns of *Necturus* and *Proteus*. In *Necturus* eggs are laid singly, attached to the undersurfaces of large rocks, as in plethodontids and salamandrids, but unlike ambystomatids, whereas *Proteus* gives birth to live young, as in *Salamandra* (see Boyden and Noble 1933).

The precise relationships of proteoids to the other more derived salamanders is uncertain. If truly primitive, the higher chromosome number (see Morescalchi 1975) and lack of intervertebral postatlantal spinal nerves (see Edwards 1976) would forbid close relationship with plethodontids and salamandroids and indicate relatively early derivation from a more basal stock. In light of the advanced nature of the axial musculature and cranial osteology, however, these two characters may be secondary. The karyotype is probably a plastic, adaptive part of the phenotype, likely to change readily in response to selective pressures (see above). Although Edwards (1976, p. 313) claimed that "the spinal nerve patterns are acquired very early in ontogeny and are not affected by metamorphosis," this is only partially true. Young larvae of at least some salamandrids have spinal nerves that exit intervertebrally. This is true for small *Pleurodeles* larvae (see

Mauger 1962), as well as for the very young larvae of *Triturus vulgaris* and larvae within the oviducts of *Salamandra* (personal observation). This shows the strong possibility that the spinal nerve patterns of proteoids are a secondary, paedomorphic phenomenon.

At present it is not possible to be very specific as to times of origin. I prefer, tentatively, to derive proteoids from the primitive stock that eventually gave rise to the plethodontoids and salamandroids, but prior to the divergence of the two latter groups (see Fig. 104).

ix) Batrachosauroididae Auffenberg 1958

CONTENT. *Batrachosauroides* Taylor and Hesse 1943, *Opisthotriton* Auffenberg 1961, *Prodesmodon* Estes 1964, *Palaeoproteus* Herre 1935, ?*Piceoerpeton* Meszoely 1967.

RELATIONSHIPS AND OCCURRENCES. *Batrachosauroides dissimulans*, based on a single complete skull, now lost, from the middle Miocene of Texas, was named and described by Taylor and Hesse (1943). These authors referred the genus questionably to the Salamandroidea of Noble (1931), as closest to the amphiumids. Auffenberg (1958) later referred vertebrae and atlantes from Texas to the species and also erected a new monotypic family, the Batrachosauroididae, which he placed in the Salamandroidea. Estes (1963) reported an atlas of *B. dissimulans* from the lower Miocene of Florida. A new species, *B. gotoi*, from the lower Eocene of North Dakota was named by Estes (1969a). It was based on a trunk vertebra, with dentaries of aspect similar to those of *B. dissimulans* being referred.

Auffenberg (1961) named and described a new genus and species from the Lance Formation of Wyoming, *Opisthotriton kayi*, and also referred lower Paleocene material from Montana to the species. *O. kayi* was based on a trunk vertebra, with atlantes and cranial material being referred. Estes (1964) showed subsequently that the figured maxilla belonged to *Scapherpeton tectum*, however. Auffenberg (1961, p. 464) assigned *O. kayi* to the Salamandridae on the basis of the opisthocoelous centra, but stated that it might "eventually be assigned to the *Plethodontidae* [sic], or to an extinct family."

Working with more extensive material from the Lance Formation, Estes (1964) provided figures and detailed descriptions of *Opisthotriton*. Numerous vertebrae, atlantes, vomers, dentaries, maxillae, and premaxillae were referred to the species *O. kayi*. Estes noted resemblances to desmognathines (with which he provisionally classified the genus) and also to *Necturus*. *Opisthotriton* is known from other Upper Cretaceous horizons: Hell Creek Formation, Kirtland and Fruitland formations, Upper Milk River Formation (= Eagle Formation), Oldman Formation (= Judith River Formation), and Judith River Formation (Estes et al. 1969, Sahni 1972, Fox 1972, 1976).

Estes (1969a) classified *Opisthotriton* with *Batrachosauroides* in the Batrachosauroididae, which was claimed to be related to the Scapherpetontidae. Both of these families were placed in the Ambystomatoidea, along with ambystomatids and plethodontids. At the same time, a skull of *Opisthotriton* from the upper Paleocene Polecat Bench Formation was figured and described. Estes (1975) later argued that batrachosauroidids were related to proteids, a conclusion that my findings strongly support (see above).

Prodesmodon copei was named and described from material from the Upper Cretaceous Lance Formation, the type specimen being a trunk vertebra (Estes 1964). Atlantes, premaxillae, maxillae, and dentaries were referred to the species, which was tentatively classified in the Plethodontidae. Subsequently, Estes (1969c) classified *Prodesmodon* with the Lower Cretaceous *Prosiren* in the Prosirenidae. This was done on the basis of the supposed common possession of unique jaw material. I have shown elsewhere (Naylor 1978a) that jaw elements have been incorrectly ascribed to *Prodesmodon* and that the dentaries named *Cuttysarkus* are properly referred to *Prodesmodon*, as is a newly discovered vomer (UA 12095). These elements are very similar to those of *Opisthotriton*, as are the vertebrae, and *Prodesmodon*, as reinterpreted, is a member of the Batrachosauroididae (see Naylor 1976, 1978a), and includes *Cuttysarkus* as a junior synonym.

Herre (1935b) named and extensively described *Palaeoproteus klatti* from the middle Eocene Geiseltales browncoal. This species is known from a series of partial and complete skeletons and was referred by Herre to the Proteidae. It is elongate with small limbs and the skull is long and narrow, with the bones being relatively robust and solidly sutured. Prefrontals and nasals are lacking and there are very long premaxillary spines (compare *Opisthotriton* in Estes 1969a, fig. 4). Herre's figure (1935b, Abb. 6) shows that the parasphenoid is broad and posteriorly produced, as in proteids and batrachosauroidids (see also Estes 1975). Only a single element is found in the *fenestra ovalis*. This was called an "operculum" by Herre, but it is undoubtedly a columella, as elsewhere he refers to the columella of *Proteus* as an operculum.

Estes et al. (1967) later named and described a new species of *Palaeoproteus*, *P. gallicus* from the Paleocene of France. At the same time, they questionably referred the genus to the Salamandridae on the basis of the suggested approach to opisthocoely, forked ribs, wide separation of the head and trochanter in the femur, and the "general shape" and robustness of the cranial bones. The figured atlas of *Palaeoproteus* is all but identical to those of *Opisthotriton* and *Prodesmodon*, while the dentary is very similar in the three genera (Estes et al. 1967, figs. 1 and 3). Estes et al. (1967) noted the resemblances of *Palaeoproteus* to *Opisthotriton*, and Estes (1969a) recognized the same close similarity and probable relationship, but did not formally place *Palaeoproteus* within the Batrachosauroididae. Based on the data presented by Herre (1935b) and Estes et al. (1967), the conclusion that *Palaeoproteus* is to be classified with the batrachosauroidids is all but inescapable. Larsen and Guthrie (1974) suggested that *Palaeoproteus* is related to the Proteidae. There are certainly similarities, but even more are evident in comparison of the genus with batrachosauroidids. The resemblances of *Palaeoproteus* to proteids are, however, further evidence of the relationship between these two families.

Abundant material of *Piceoerpeton* from the Paleocene Ravenscrag Formation of Saskatchewan indicates that this genus is probably a member of the Batrachosauroididae (Naylor and Krause, in prep.). As argued by Estes (1975) and discussed above, the Batrachosauroididae are to be united with the Proteidae in the superfamily Proteoidea.

x) Salamandridae Gray 1825

CONTENT. *Salamandra* Laurenti 1768, *Chioglossa* Bocage 1864, *Pleurodeles* Michahelles 1830, *Tylototriton* Anderson 1871, *Salamandrina* Fitzinger 1826, *Notophthalmus* Rafinesque 1820, *Taricha* Gray 1845, *Cynops* Tschudi 1838, *Paramesotriton* Chang 1935, *Hypselotriton* Wolterstorff 1934, *Pachytriton* Boulenger 1878, *Triturus* Rafinesque 1815, *Neurergus* Cope 1862, *Euproctus* Gené 1838. In addition to these extant genera, the following fossil genera have been named: *Palaeosalamandra* Herre 1949, *Praesalamandra* Brunner 1957, *Megalotriton* Zittel 1888, *Voigtiella* Herre 1949, *Palaeosalamandrina* Herre 1949, *Palaeopleurodeles* Herre 1941, *Dehmiella* Herre and Lunau 1950, *Polysemia* goldfuss 1831, *Heliarchon* von Meyer 1964, *Grippiella* Herre 1949, *Tischleriella* Herre 1949, *Chelotriton* Pomel 1853, *Oligosemia* Navas 1922, *Archaeotriton* von Meyer 1859, *Brachycormus* Herre 1949, *Heteroclitotriton* De Stefano 1903, *Koalliella* Herre 1950.

FOSSIL RECORD. Except for a French Miocene record of *Chioglossa* reported by Estes and Hoffstetter (1976), the fossil occurrences of salamandrids and the possible relationships of the taxa have been discussed under the anatomical descriptions of the individual species above.

RELATIONSHIPS. Intergeneric relationships within the Salamandridae have been uncertain. Bolkay (1928), basing his conclusions on cranial osteology, believed *Euproctus* to be primitive, not only to salamandrids, but with respect to ambystomatids as well. This scheme is in conflict with other anatomical evidence and with logical inference of phylogeny.

Nevertheless, Bolkay (1928) did conclude that *Salamandra* and *Chioglossa* were primitive with respect to the other newts. Herre (1935b) also believed that these two genera were the most primitive members of their family.

Noble (1931) considered the following features to be primitive for salamandrids:

1. Bony frontosquamosal arch.
2. High neural crests.
3. Long ribs.
4. Four-pronged basihyal in hyobranchium.
5. Single, simple *rectus abdominis*.
6. Presence of an *obliquus internus*.

These features are exhibited by one or another of the newts, notably *Tylototriton*. With the exception of the fourth feature, it is all but certain that all are derived. On the basis of ex-group comparisons, these features are shown to be apomorphic for the Salamandridae. As *Salamandra* and *Chioglossa* lack these character states, which are also lacking in more primitive families (hynobiids, ambystomatids, and plethodontids), it is not reasonable to assume secondary loss to account for the conditions in these two genera (see below).

In the most recent study of the intrafamilial relationships of salamandrids, Wake and Özeti (1969) developed a detailed generic phylogeny. Although probably in large part correct, certain of their results reflect misinterpretations and an over-reliance on a single adaptational system, the hyobranchium. I suggest that their 40 characters fall into the following categories (numbering follows Wake and Özeti 1969):

A. Those probably correctly identified as primitive or derived and, therefore, of value in phylogenetic reconstruction:

1. Separate premaxillae.

13. Presence or absence of the second basibranchial (bb2).

14. Presence or absence of the epibranchial.

15. One or two pairs of radii on first basibranchial.

16. Presence or absence of an interradial cartilage. This is, however, linked to the number of pairs of radii and, therefore, not deserving of status as a separate character.

B. Those correctly identified as primitive or derived, but carrying little or no phylogenetic information:

7. Loss of the fifth toe. This is found only in *Salamandrina* and is thus an autapomorphy as well as a loss character (see Hennig 1966, Hecht and Edwards 1976).

8. Reduction of the lungs. This is convergent in species inhabiting mountain streams (see Wilder and Dunn 1920).

12. Reproductive pattern. Only *Salamandra* gives birth to live young; the other genera lay eggs. This feature is, therefore, an autapomorphy.

C. Those of equivocal status and, therefore, of low phylogenetic value:

5. Ossification of the operculum.

6. Presence of caudosacral ribs (this may be truly primitive, however).

10. Size of eggs.

17. Ossification of the first basibranchial.

18. Ossification of the first ceratobranchials.

D. Those incorrectly, or not identified as to primitive or derived state:

2. Frontosquamosal arch. This structure is also lacking from all other families, as well as from *Salamandra* and *Chioglossa*. It is, therefore, not reasonable, parsimonious, or logical to consider the structure primitive with respect to the Salamandridae. The frontosquamosal arch gives the newt skull a superficially archaic (or "primitive") aspect, but bears little resemblance to the structures of truly primitive amphibians (see Romer 1966, Bolt 1969).

3. Length of maxillae. As short maxillae are found in all of the more primitive families of salamanders, as well as in certain salamandrids, it is not reasonable to assume a long maxilla to be primitive to the family.

4. Medial contact of nasals. The nasals overlap the elongate premaxillary spines in some newts, but this is a highly derived condition secondarily convergent upon that of hynobiids (compare ambystomatids, plethodontids, and salamandrines).

9. Texture of the skin. As rough skin was correlated with features incorrectly judged to be primitive (e.g., the frontosquamosal arch, nasals in medial contact, and elongate maxillae), it too was considered primitive. As the correlated features are more reasonably derived and because rough skin is lacking in all of the more primitive families, there is no evidence for assuming rough skin to be primitive for the Salamandridae.

11. Courtship pattern. The pattern of *Euproctus* was assumed to be primitive on the basis of Salthe's (1967) work. However, courtship

patterns within the Salamandridae compared with those of other families makes this conclusion unlikely. Courtship in *Euproctus* differs markedly from that of other newts, with the male capturing the female by means of his tail. It is probable that the pattern of *Euproctus* is highly derived, adapted to the mountain streams and rivers in which it lives, and it is not reasonable or parsimonious to hypothesize plesiomorphy. The courtship of *Euproctus* could well be derived from that of *Triturus*, which also uses the tail as an important component in courtship, although in a different fashion (Salthe 1967). The courtship of *Salamandra* and *Chioglossa* (Salamandrinae) and of *Tylototriton*, *Pleurodeles*, and *Salamandrina* (Pleurodelini) is the same (capture from beneath with the anterior limbs, see Salthe 1967) and correlated with structural primitiveness. It is probably the most primitive for the family (see also Salthe and Mecham 1974).

40. Contact of the maxilla and pterygoid. This feature is unique to a few Asian newts, found in no other families of salamanders (except one ambystomatid), and basically different from maxillary-pterygoid contact in other amphibians. It is, therefore, a derived character state.

E. Those characters coming from a single functional system (the hyobranchial apparatus) and, therefore, probably not deserving of minute subdivision. These include the remainder of the characters.

Clusters developed from computer analysis do not necessarily reflect phylogenetic events, especially if the majority of the features come from a single integrated system. Before clustering can have phylogenetic meaning, the characters must be interpreted.

Otherwise the phenetic groupings will not accurately reflect evolution. This is evident in the grouping by Wake and Özeti (1969) of *Salamandrina* with *Salamandra* and *Chioglossa*. The protrusible tongue of the former is all but certainly convergently (and only superficially) similar to that of the salamandrines. The frontosquamosal arch, cranial structure, separation of a *rectus abdominis profundus*, lack of second basibranchial, high neural crests with robust capping plates, structure of the *dorsalis trunci* and *subvertebralis*, and the presence of long ribs all indicate the close relationship of *Salamandrina* with *Pleurodeles* and *Tylototriton*. As recognized by almost all previous workers (Boulenger 1882, Cope 1889, Dunn 1926, Bolkay 1928, Herre 1935b, von Wahlert 1953, and Thorn 1968), "*Salamandrina* is merely a European newt lacking the fifth toe" (Noble 1931, p. 475) and closely allied to *Pleurodeles* and *Tylototriton*.

I separate the Salamandridae into two subfamilies, the Salamandrinae and Pleurodelinae, which are distinct in terms of shared and derived features. The Salamandrinae consists of only *Salamandra* and *Chioglossa*, and differs from the newts in terms of cranial anatomy, the vertebral column, and trunk musculature. The subfamilies seem to share a sister-group relationship (see Fig. 101) of descent from a common ancestor. Each lineage subsequently became divergently specialized, but salamandrines retained the majority of the relatively more primitive character states. Salamandrines and the *Pleurodeles* group (tribe Pleurodelini) share unfused premaxillae in the adult, some members with two pairs of radii on the first basibranchial, some members with at least partial differentiation of the *rectus abdominis*, and similar courtship patterns. To these probably primitive features may be added, questionably, the elongate, somewhat divergent anterior flexures in the *dorsalis trunci* of *Salamandra* and *Pleurodeles*.

Salamandrines are primitive as regards the posterior flexures of the subvertebral musculature, lack of a frontosquamosal arch, structure of the auditory apparatus (see Reed 1920, Monath 1965), and general flexibility and structure of the snout. The *Pleurodeles* group is probably primitive as regards the free *rectus abdominis profundus* in *Salamandrina* and *Tylototriton*.

I subdivide the Pleurodelinae into two tribes: the Pleurodelini for *Pleurodeles*, *Salamandrina*, and *Tylototriton*, and the Triturini for the remainder of the newts (see Table 3). The relationships of these tribes are shown in the tentative cladogram of Figure 101. The triturines are derived with respect to the *Pleurodeles* group. They have (excepting *Taricha*) lost the second pair of radii from the first basibranchial, the premaxilla is a single element, their patterns of courtship are evidently highly modified (see data in Salthe 1967), and their trunk musculature is derived. Unity of the tribe is also shown by the presence of tetrodotoxin in many of the included genera (see Brodie et al. 1974): *Notophthalmus*, *Taricha*, *Cynops*, and *Paramesotriton*.

In light of studies tending to indicate close relationships within the Asian species (except *Tylototriton*) on the one hand, and between *Notophthalmus* and *Taricha* on the other, and in the absence of positive controverting evidence, these may be considered to form natural groups. Özeti and Wake (1969) showed similarities in the hyobranchial apparatus within the two, and courtship data seem to indicate unity of the North American and Asian species into two generic groups: the *Notophthalmus* group (with *Notophthalmus* and *Taricha*) and the *Cynops* group (*Cynops*, *Paramesotriton*, *Pachytriton*, and *Hypselotriton*). Tihen (1974) has described fossils that indicate close relationship between *Notophthalmus* and *Taricha*. The trunk musculature of *Cynops* and *Paramesotriton* is similar (see above) and, although somewhat different, the musculature of *Notophthalmus* is derivable from that of *Taricha* by paedomorphosis.

The exact relationships and sequences of splitting of the *Cynops* and *Notophthalmus* groups are uncertain. Courtship data (with capture in the North American newts), the strong frontosquamosal arch in the *Notophthalmus* group, and the retention of a second pair of radii in *Taricha* tend to indicate that the North American species are more primitive. Included in the *Cynops* group are members with great variability in the development of the frontosquamosal arch (Chang and Boring 1935). As this reduction seems, in this case, to be secondary, the condition in the *Notophthalmus* group is more primitive. Courtship in the *Cynops* group resembles that of *Triturus*, with no capture by the males (see Salthe 1967). I suggest that the *Notophthalmus* group split from the stock that eventually gave rise to *Triturus* and its allies prior to the divergence of the *Cynops* group (see Fig. 101), but this is tentative.

The remaining European newts can be separated into two apomorphic generic groups: the *Triturus* group (with *Triturus* and *Neurergus* included) and the *Euproctus* group (only *Euproctus*). *Neurergus* is very close to *Triturus*, as recognized ever since Cope (1862) proposed the former genus (see Wolterstorff 1926, Bolkay 1928, Herre 1932, Özeti and Wake 1969, Wake and Özeti 1969). I show the *Triturus* and *Euproctus* groups as the most derived of the Salamandridae and sharing a sister-group relationship (Fig. 101). Both groups show variability and tendency to loss of the frontosquamosal arch. In view of the likelihood of the primitive position of the Pleurodelini within the Pleurodelinae, it seems that those newts lacking a fully bony arch have undergone secondary loss, as is corroborated by the presence of a ligamentous arch as a replacement (except, apparently, in *Triturus cristatus*). Courtship data also indicate the derived nature of these two groups (see Salthe 1967), with *Euproctus* being perhaps derivable from *Triturus* in this regard.

Nevertheless, the relationships of these two generic groups is tentative. Herre (1935b) suggested that *Euproctus* was most closely related to the Asian *Pachytriton*. In this regard, it is noteworthy that of the six different clustering analyses run by Wake and Özeti (1969) all produced a phenogram showing *Pachytriton* and *Euproctus* as the most similar, and the position of *Euproctus* remains uncertain. My proposed classification of the Salamandridae is given in Table 3.

The relationships of the Salamandridae to the other families have long been uncertain. Cope (1889) considered them to have been derived from anbystomatid ancestry, whereas Dunn (1926) suggested they were structurally ancestral to plethodontids. Noble (1931) followed Dunn, also noting that the "body musculature" of *Salamandra* was similar to that of plethodontids and deriving salamandrids directly from hynobiids. Herre (1935b) derived salamandrids and plethodontids from a common ancestor.

The close relationship of plethodontids and salamandrids is presently rejected (see Laurent 1947, Larsen 1963, Regal 1966, Wake 1966). As the relationship was largely, or exclusively, based on the disposition of the vomerine and parasphenoid teeth, rejection was proper. However, my studies demonstrate that there is, in fact, a close relationship between salamandrids and plethodontids, although not precisely of the sort envisaged by earlier workers.

Salamandra shows certain resemblances to plethodontids. As shown above, the opisthocoelous condition is owing to posterior pull on each posterior cotyle. Plethodontids have posterior flexures or posterior basapophyseal muscles, *Salamandra* retains posterior flexures, and all salamandrids and certain plethodontids are opisthocoelous. The premaxilla develops as a fused element in embyronic *Salamandra* (personal observation) and this has been shown to be the primitive form of development in plethodontids (see Wake 1966). Certain newts (*Tylototriton* and *Salamandrina*) as well as *Chioglossa* retain a free *rectus abdominis profundus* extending from hyobranchium to pelvis, which is shared with plethodontids. In addition, the cranium of salamandrids is readily derivable from that of *Plethodon*, except as regards the vomer and auditory apparatus (see Reed 1920, Monath 1965).

Schaeffer's (1941) study of the tarsus in amphibians and reptiles shows similarity between this unit in plethodontids and salamandrids that is not shared with other urodeles. Although he claimed that the tarsus of *Salamandra* was more derived than that of the newts, this cannot be supported. *Salamandra* retains four elements in the tarsale series, whereas the newts (e.g., *Triturus*) have only three. The tarsus of salamandrids (e.g., *Salamandra*) and plethodontids (e.g., *Desmognathus*, see Schaeffer 1941, fig. 2) is composed of the same number and kinds of elements, situated in the same way. In both families, tarsale one and tarsale two have fused into a single transverse unit supporting the first and second digits. By contrast, ambystomatids have a longitudinally elongate element formed by fusion of the first centrale and first tarsale in this position.

Lombard (1977) divided the inner ears in the Caudata into two sorts, "aquatic" and "terrestrial," noting that only plethodontids and salamandrids have a "terrestrial" kind of inner ear. He also stated (p. 130) that the inner ear of these two families is "the most paedomorphic and the most elaborate and novel" amongst the urodeles, and that "the novel aspects [of the inner ear] found in the two groups are unique in vertebrates" (p. 131). Although, citing Edwards (1976), Lombard concluded that these unique resemblances were convergently developed in plethodontids and salamandrids, in light of the other evidences they are probably owing to apomorphy.

I suggest that the most reasonable theory to account for these resemblances is that plethodontids and salamandrids have descended from a common ancestor, with each lineage having become divergently adapted. The two families share several apomorphic character states, whereas the states shared by plethodontids and ambystomatids are primitive with respect to non-cryptobranchoid salamanders. Although this suggestion of relationship (see Fig. 103) may seem a radical and/or retrogressive step, it does not differ greatly from ideas presently accepted. That is, it is here admitted that plethodontids and ambystomatids are closely related, the change comes in also relating the former to salamandrids. There is good evidence for this latter contention (see above) and I group the Salamandridae with the Plethodontidae (see below and Table 4), although in separate superfamilies, not in an attempt to depreciate the resemblances of plethodontids and ambystomatids, but in order to emphasize the derived character states rather than the primitive. Plethodontids and salamandrids (as well as proteoids and sirenids) are members of a group having undergone a fundamental adaptive shift in the locomotory system.

xi) Sirenidae Gray 1825

CONTENT. *Siren* Linnaeus 1766, *Pseudobranchus* Gray 1825, *Habrosaurus* Gilmore 1928.

FOSSIL RECORD. Estes (1964, 1965b) described the earliest known sirenid, *Habrosaurus dilatus* Gilmore 1928, in detail. This species is known from the Upper Cretaceous and Paleocene of central North America (Estes 1964, 1976, Estes et al. 1969, Fox 1972), and includes the species *Adelphesiren olivae*, named by Goin and Auffenberg (1958) from the Lance Formation, as a junior synonym. Estes (1964) assigned ceratobranchials, dentaries, premaxillae, maxillae, palatal tooth plates, atlantes, and numerous trunk vertebrae from the Lance Formation (Upper Cretaceous, Wyoming) to *Habrosaurus*.

Dentaries of *Habrosaurus* are similar in overall shape to those of *Siren*, but whereas those of living sirenids have teeth only on the coronoid, *Habrosaurus* retains teeth on the dentary. These are robust, non-pedicellate, and provided with flat, crushing crowns. Also unlike Recent sirenids, *Habrosaurus* has toothed maxillae and premaxillae. In *Siren*, maxillae are reduced to tiny slivers of bone (see Larsen 1963) and the premaxillae are delicate and edentulate.

Atlantes assigned to *Habrosaurus* differ from those of *Siren* in their possession of a broad, blunt odontoid process, but this is a matter of degree (compare Fig. 11, Estes 1964, fig. 37). Vertebrae (Estes 1964, pp. 74-77) have the relatively high neural crests and aliform processes that are also diagnostic of *Siren* and *Pseudobranchus*. The genera differ in "the invariable presence in [*Habrosaurus*] . . . of well-developed basapophyses on the ventral border of the anterior cotyle, and the lack of high, fin-like neural spine [= neural crest] and aliform processes" (Estes 1964, p. 79). The latter part of the quotation does not mean that aliform processes and neural crests are lacking, but that they are lower than in living sirenids. Estes (1964, p. 79) suggested that either the basapophyses of *Habrosaurus* are incorporated into the ventral lamellae in *Siren*, or "the extensions of the transverse processes replace, rather than obscure, the basapophyses."

Although either interpretation is possible, my study of the trunk musculature indicates that the "basapophyses" of *Habrosaurus* are secondary derivations from the ventral lamellae of the transverse processes. The muscle projecting from the ventral lamella in *Siren* is not homologous to the anterior basapophyseal muscles of other salamanders (see above), indicating that the structures of *Habrosaurus* are probably not true basapophyses. If this is so, *Habrosaurus* cannot form an ancestor-descendant relationship with *Siren* or *Pseudobranchus*, but must represent an early, divergent lineage. This conclusion is partially corroborated by the massive dental apparatus of *Habrosaurus*.

Except for a Paleocene record (Estes 1976) of *Habrosaurus*, all Tertiary fossil sirenids are referable to the living genera. Goin and Auffenberg (1955, 1957) studied the known fossil material and named several new species. They recognized *Siren dunni* from the middle Eocene of Wyoming, *S. hesterna* from the lower Miocene of Florida (additional specimens were reported by Estes 1963), and *S. simpsoni* from the Pliocene of Florida. Holman (1966) noted material referred to *Siren* species from Miocene rocks in Texas. In addition to these fossil species, *Siren lacertina* is known from the Pleistocene of Florida (Goin and Auffenberg 1955, Lynch 1965).

Two fossil species of *Pseudobranchus* were named by Goin and Auffenberg (1955): *P. robustus* from the Pleistocene and *P. vetustus* from the Pliocene of Florida. Holman (1962) reported additional specimens of *P. robustus* from the Pleistocene of Florida and Lynch (1965) referred material from the same age to *Pseudobranchus* cf. *robustus*, noting that, as there is overlap with the Recent *P. striatus*, the species *P. robustus* may not be valid. The fossil material of *Siren* and *Pseudobranchus* consists of vertebrae and is of interest only in that it documents paleozoogeographic distributions. It provides no information as to the relationships of the family.

RELATIONSHIPS. The origins and relationships of sirenids have been uncertain. Cope (1889) classified the family in a distinct order, Trachystomata, which he indicated as being derived from the Urodela. Goin and Goin (1971) attempted to reinstate this order, as it is claimed to be "sharply distinct" from the other families of salamanders. However, in light of the numerous and detailed resemblances between sirenids and other urodeles, and because no data in support of the contention have been provided, this step has not been followed (see also Estes 1965b).

Dunn (1922) noted that the relationships of *Siren* and *Pseudobranchus* were unknown. Noble (1931) continued to classify them in a separate suborder, but observed that their lack of cloacal glands indicated external fertilization and noted the possibility of derivation from hynobiids. In his figure 145, however, tentative relationship to ambystomatids is indicated. Herre (1935b) argued for a salamandrid ancestry. Reed (1920) considered the auditory apparatus to relate sirenids to the salamandrid newts, whereas Larsen (1963) tentatively derived the family from a plethodontid ancestor.

As can be seen, almost every possibility has been suggested and, at present, sirenids are classified in a separate suborder of uncertain affinities (Regal 1966, Wake 1966, Edwards 1976). Most recently, Putnam (1976) suggested that sirenids are more primitive than cryptobranchoids. This was based on the claimed similarity between the hearts of lungfish and sirenids. What this contention overlooks is that lungfish and salamanders are not at all related, that sirenids and lungfish share similar sorts of habitats, and that all other features of sirenids argue against the conclusion. The resemblances in the heart of sirenids and lungfish are owing solely to adaptive convergence and indicate nothing about the relationships of sirenids.

Previous workers have commented on the similarities between sirenids and the salamandrid newts, and it is here argued that sirenids are derived from a salamandrid ancestor. Noble (1931) noted the marked lateral positioning of the olfactory lobes in *Siren* and newts, presumably a derived condition. Reed (1920) and Herre (1935b) believed sirenids to be derived from salamandrids.

The otic region is of major interest (see Kingsbury and Reed 1909, Reed 1920, Larsen 1963, Monath 1965). The middle ear of *Siren* is constructed in such a way as to indicate derivation from a normally metamorphosing ancestor that had completely lost a free, functional columella, as is the case in newts. Unlike all other paedogenic salamanders, sirenids lack the *stylus columella*. The operculum remains as a free element in the *fenestra ovalis* and maintains a connection to the *levator scapulae*. This is remarkably similar to the situation in newts. Other larval aquatic salamanders of more primitive structure have the columella as the mobile unit in the middle ear, serving to transmit vibrations from the suspensorium (e.g., proteids, amphiumids, and cryptobranchids). In *Siren* the operculum has been secondarily modified for fully aquatic sound reception (see Kingsbury and Reed 1909), with a connection extending between it and the hyobranchium.

Estes (1964, 1965b) noted the marked resemblance between newts and sirenids in the high neural crests and aliform processes of the vertebrae. Aliform processes are not unique to sirenids (contra

Auffenberg 1959), but a derived character shared with newts. Edwards' (1976) descriptions of the patterns of spinal nerve exits show unique identity in sirenids and salamandrids (with all nerves usually exiting intravertebrally). Estes (1964, p. 79) remarked that the arrangement of the vomerine teeth in *Habrosaurus* "closely resembles the pattern of vomerine teeth seen in [the] Salamandridae, and may indicate relationship to the Salamandroidea." Sirenid cranial anatomy is of larval aspect (see Larsen 1963, Estes 1965b) and, although modified, does not debar a salamandrid ancestry.

My dissections show detailed and marked similarity in trunk musculature between sirenids and newts (see descriptions above). It is evident that *Siren* has become secondarily adapted to aquatic life, developing musculature for anguilliform locomotion in a manner convergent with, but quite different from, *Amphiuma*. The structure of the vertebral column and associated musculature of *Siren* demands derivation from a fully opisthocoelous ancestor with greatly simplified trunk musculature. Early derivation from primitive salamander stock (Cryptobranchoidea and Ambystomatoidea) is forbidden by these observations.

The epaxial myomeres are reminiscent of the condition in newts, and are probably only derivable from such an opisthocoelous ancestor. Hyperapophyseal muscles are like those of newts having high neural crests and aliform hyperapophyses. The subvertebral musculature is readily derivable from that of newts (e.g., *Notophthalmus*), but not from any more primitive ancestor (compare descriptions and figures of hynobiids, ambystomatids, and plethodontids). Superficially, the anterior projections from the ventral lamellae of *Siren* appear to be homologous to anterior basapophyses, but the structure of the associated septa and muscle fibers and the absence of posterior flexures show that no homology exists between them and the true anterior basapophyses of cryptobranchoids and ambystomatoids.

In *Siren* a strap-like septum extends forward from each anterior projection of the ventral lamella. Muscle fibers fan anteriorly from these septa onto the ventral surfaces of the next anterior ventral lamellae (see Fig. 87). By contrast, in those species possessed of true anterior basapophyses a more or less vertical septum extends forward and another septum backward from each basapophysis. The anterior septum, and its associated musculature, forms the anterior basapophyseal muscle, whereas the posterior septum forms part of the posterior (or transverse process) flexure. The anterior basapophyseal muscle is, in addition, associated with the lateral surface of the centrum and not with the transverse process.

This ventral lamellar muscle of *Siren* is, however, readily derivable from the pattern exhibited by newts (e.g., *Notophthalmus*) that have well-developed, plate-like ventral lamellae on each transverse process. All that is necessary is that fibers inserting on the anterior edge of one lamella come to extend forward and attach to the ventral surface of the next anterior ventral lamella.

The *transversus* of sirenids is, seemingly, of unique structure, its dorsal portion extending into the *subvertebralis* and attaching to the lateral edges of the ventral lamellae and centra by tough fascia. In newts the *transversus* attaches to the centra, extending under the *subvertebralis* and ventral lamellae. In *Paramesotriton* (see Fig. 77) the *transversus* also attaches to the ventral lamellae in places, but the *transversus* is still located ventral to the *subvertebralis*. The situation in the two families would, therefore, seem to be quite different. The more ventral part of the *subvertebralis* in *Siren*, however, is a secondary development owing to the neomorphic ventral lamellar muscles. The *subvertebralis* proper remains dorsal to the ventral origins of the *transversus*, as in *Paramesotriton* and other newts.

The lateral abdominal musculature of *Siren* consists of four lateral layers and a simple ventral *rectus abdominis*. This condition is explainable as a neotenic adaptation for aquatic, anguilliform locomotion and is closely approached by newts such as *Notophthalmus* and *Triturus cristatus*.

Although the method of reproduction is not known, the lack of spermathecae in female sirenids has usually been interpreted as evidence for external fertilization, as in cryptobranchoids (Noble 1931). However, owing to the fact that the eggs of *Siren* and *Pseudobranchus* "are deposited either in small groups or singly and not enclosed within the common envelope of jelly so characteristic of the Hynobiidae" (Boyden and Noble 1933, p. 3), it is probable that fertilization is internal. This sort of egg-laying recalls that of the salamandrids and "the eggs resemble those of some newts more than they do those of any other salamander" (Boyden and Noble 1933, p. 3). In the live-bearing *Salamandra* sperm enters directly into the oviducts to fertilize the eggs and perhaps sirenids have a similar sort of fertilization. Boyden and Noble (1933) note the possibility that the cloacal glands of sirenids have been lost owing to paedomorphosis.

The high chromosome number of sirenids (*Pseudobranchus* with a count of n=32; *Siren lacertina*, n=26; and *S. intermedia*, n=21; see Morescalchi 1975) has been used as evidence for a more primitive status than is here argued (Morescalchi 1975, Edwards 1976). However, Morescalchi and Olmo (1974) demonstrate the possibility that sirenids are tetraploid and such an interpretation fits much better with the other anatomical evidences. As noted by Morescalchi (1973), karyology must be considered together with data from other systems and not as an infallible guide to relationships (see also above). There is a further, but very tenuous, piece of evidence from karyology. In *Siren intermedia* and *Triturus helveticus* it is known that only the female undergoes recombination (Watson and Callan 1963, Leon and Kezer 1974), perhaps indicating affinity of their two families.

It is, therefore, reasonable to conclude that sirenids are derivable from some fully opisthocoelous ancestor, which had lost complexity in the *subvertebralis* and *dorsalis trunci*. There are few, if any, features debarring extant newts from a position of structural ancestry. Although contemporaneous species cannot, of course, form any sort of an ancestor-descendant relationship, it is likely that if known the ancestor of the Sirenidae would be classified as an apomorphic salamandrid without modifying the definition of the Salamandridae. In order to reflect this relationship (see Fig. 103), I classify the Sirenidae with the Salamandridae in the superfamily Salamandroidea.

xii) Prosirenidae Estes 1969

CONTENT. *Prosiren* Goin and Auffenberg 1958, *Albanerpeton* Estes and Hoffstetter 1976, ?*Ramonellus* Nevo and Estes 1969.

OCCURRENCES AND RELATIONSHIPS. *Prosiren elinorae* is known from the Lower Cretaceous Trinity Formation of Texas, where it is represented by atlantes, vertebrae, premaxillae, dentaries, and a single humerus (see Estes 1969c, figs. 1 and 2). It was originally described as a sirenid by Goin and Auffenberg (1958), but Estes (1969c) showed that it was referable to no extant family. The jaw elements are of the same sort as those assigned by Estes (1964) to *Prodesmodon* and were used as the basis for uniting *Prosiren* and *Prodesmodon* in a new family, the Prosirenidae (Estes 1969c). The supposed presence of genera with different sorts of vertebrae (*Prosiren* being amphicoelous and *Prodesmodon* opisthocoelous) was held to document the relationship of plethodontids and ambystomatids, with which the Prosirenidae were placed in the Ambystomatoidea.

Nevo and Estes (1969) subsequently added *Ramonellus longispinus* from the Lower Cretaceous of Israel to the Prosirenidae, although questionably. *Albanerpeton inexpectatum*, from the Miocene of France, is represented by extensive vertebral, appendicular, and cranial material. This has been described by Estes and Hoffstetter (1976), who note that an atlas from the Jurassic of Europe described by Seiffert (1969) is also from a prosirenid. *Albanerpeton* has the unique dentaries, maxillae, premaxillae, and humeri of *Prosiren*, as well as comparable vertebrae, although there is developed an "atlas-axis" complex unknown in other salamanders.

Atlantes, premaxillae, maxillae, dentaries, and cranial roofing bones very like those of *Albanerpeton* are known from the Upper Milk River Formation (Upper Cretaceous), Alberta. Jaw material previously called *Prodesmodon* is known from many Upper Cretaceous formations in North America (Estes 1964, 1969c, Estes et al. 1969, Sahni 1972, Fox 1972, 1976, Naylor 1978a), as well as from the Paleocene of Alberta (Fox pers. comm.) and Montana (Van Valen and Sloan 1965). I show elsewhere that this material is not properly referred to *Prodesmodon copei*, which is based on a vertebra (see Naylor 1978a). The jaw material is properly referred to *Albanerpeton* or a new genus near *Albanerpeton*, as shown by the atlantes from the Upper Milk River Formation. Estes and Hoffstetter (1976) provide figures and descriptions of the French prosirenid material.

The proper relationships of the Prosirenidae are uncertain. If they are salamanders, they are closest structurally to cryptobranchoids. The vertebrae apparently lack foramina for spinal nerves, the post-dentary bones are not fused together, and anterior basapophyses are present (although Estes and Hoffstetter [1976] note that weak posterior basapophyses are also present on some vertebrae of *Albanerpeton*).

The cranial material and "atlas-axis" complex are unique amongst salamanders, although the vertebrae appear to be similar to those of urodeles. The dentaries are small, but very robust and provided with strong non-pedicellate teeth, which apparently lack basal pits for a replacement series. There is a unique symphyseal joint of a sort unknown in other salamanders (see Estes and Hoffstetter 1976). The articular surface for the quadrate faces posteriorly from the lower jaw.

The skull of *Albanerpeton* as reconstructed by Estes and Hoffstetter (1976, fig. 4) is high, and the roofing bones are also not of salamander aspect. The limb elements are unique in having well-ossified epiphyseal regions. The "atlas-axis" complex is formed of three vertebrae. The atlas is salamander-like anteriorly, but lacks posterior zygapophyses and has a concavity posteriorly for articulation with the "axis." This latter element is composed of two vertebrae fused together. The more anterior vertebra lacks a neural arch and forms a projection from the front of the third. Anterior zygapophyses are lacking from the third vertebra, the anterior of the neural arch being raised and expanded so as to abut the atlas (see Estes and Hoffstetter 1976, figs. 1 and 2, and accompanying descriptions).

If, in fact, prosirenids are salamanders, they are an early, divergent stock from very primitive ancestry. They are referable to no known superfamily, and I classify them *incertae sedis* within the Caudata (see Table 4).

xiii) Familial Synthesis

From the information and inferences on the inter- and intrafamilial relationships of the Caudata presented above, it is possible to integrate these conclusions into a coherent phylogenetic reconstruction and a classification that is consistent with it (see Figs. 102, 103, and 104, and Table 4). The order may be readily divided into two subdivisions, one primitive and one derived, and each characterized by its own trends. The more primitive division includes two superfamilies, Cryptobranchoidea and Ambystomatoidea, the cladistic relationships of which are diagrammed in Figure 102.

As has been long accepted (Dunn 1926, Noble 1931), the Cryptobranchoidea are held to be a natural and monophyletic group. The family Hynobiidae is the most phenetically primitive of living salamanders, probably representing structurally the ancestral salamanders in most features (see above). By variable processes of paedomorphosis and simplification and/or complication, the remainder of known fossil and Recent salamanders are derivable from hynobiids. The Cryptobranchidae include giant aquatic derivatives from hynobiid stock, retaining the same basic subvertebral and epaxial musculature and a larval system of lateral abdominal musculature. The skull has been remodelled, but within the limits of the basic hynobiid plan.

It is likely that all other salamanders (excepting prosirenids) form a monophyletic group (sensu Simpson 1961) derived from hynobiid or hynobiid-like ancestry. Shared-derived features include internal fertilization by means of a spermatophore (where known), elongate premaxillary spines, fusion of the angular and prearticular in the lower jaw, and a reduction in chromosomal number. The most primitive superfamily in this derived assemblage is the Ambystomatoidea (scapherpetontids, amphiumids, and ambystomatids). These salamanders show development of postatlantal intravertebral exits for spinal nerves, with a morphocline as follows (see also Edwards 1976);

1. Amphiumidae: the more posterior caudal vertebrae with intravertebral exits.
2. Scapherpetontidae: ?caudosacral and caudal vertebrae with intravertebral exits.
3. Dicamptodontinae: caudosacral and caudal vertebrae with intravertebral exits.

4. Ambystomatinae: except for those of the second cervical, all exits intravertebral.

This cline could well represent a phylogenetic event, with succeeding "escapes from specialization" (Maslin 1952). Evidence from other anatomical systems does not forbid such an interpretation.

I use a cladogram (Fig. 102) to diagram the relationships of ambystomatoids and cryptobranchoids, but rather than speaking of a sister-group relationship it is more proper to derive ambystomatids *from* hynobiid ancestry (see Fig. 104). As discussed above, the sequence of splitting of amphiumids and scapherpetontids from ambystomatid or pro-ambystomatid ancestry is uncertain. Amphiumids are represented as having diverged first on the basis of the patterns of spinal nerve exits and the presence of autapomorphies, perhaps indicating a longer time since separation. Nevertheless, this interpretation is tentative.

Ambystomatoids are structurally intermediate between cryptobranchoids and the more derived subdivision of the Caudata. They are defined by a combination of characters, rather than by one or two unique characters:

1. Internal fertilization where known.
2. Low chromosome number where known (n=14 or 13).
3. Fusion of angular and prearticular in lower jaw.
4. Elongation of premaxillary spines.
5. Retention of anterior basapophyseal trunk musculature.
6. Spinal nerves partially, but not totally, intravertebral in exit.

The position of the Prosirenidae is uncertain. If properly referred to the Caudata, the family is closest to the Cryptobranchoidea (see above) and I place them *incertae sedis* (and questionably) in the primitive subdivision of the Caudata. Together the cryptobranchoids and ambystomatoids are considered to belong to a new suborder, defined on the pattern of trunk musculature. This suborder comprises the most primitive salamanders:

Order Caudata Oppel 1811

Suborder Archaeocaudata nov.

ETYMOLOGY. From the Greek ἀρχαῖος, meaning ancient, combined with the ordinal name Caudata, in reference to the suborder including the more primitive salamanders.

DIAGNOSIS. Salamanders with primitive trunk musculature, full development of anterior basapophyseal muscles and transverse process flexures subvertebrally, at least the second cervical lacking foramina for spinal nerves, and fully amphicoelous centra.

CONTENT. The families Hynobiidae, Cryptobranchidae, Scapherpetontidae, Amphiumidae, Ambystomatidae, and (questionably) Prosirenidae.

The families of the second suborder are divided into three superfamilies (see Fig. 103 and Table 4), as discussed above. These salamanders are derivable from ambystomatid or ambystomatid-like ancestry, with the Plethodontidae being the most primitive osteologically and myologically. Owing to basic trends continuing throughout the Caudata, it is difficult to produce a division of the families that holds for all anatomical systems. Cryptobranchoids, ambystomatids, plethodontids, salamandrids, and sirenids form a single morphocline in many of their features (e.g., chromosomal number, trunk musculature, cranial structure, and osteology). Nevertheless, there is clear separation in terms of the trunk musculature and vertebral column, justifying separation. The second suborder includes the more derived salamanders (see also above):

Order Caudata Oppel 1811

Suborder Neocaudata nov.

ETYMOLOGY. From the Greek νέος, meaning new, combined with the ordinal name Caudata, in reference to the suborder including the more derived salamanders.

DIAGNOSIS. Salamanders having derived and simplified trunk musculature, with complete loss of anterior basapophyseal muscles and general reduction of the *subvertebralis*. All families include opisthocoelous species, or are derivable from opisthocoelous ancestry.

CONTENT. The families Proteidae, Batrachosauroididae, Plethodontidae, Salamandridae, and Sirenidae.

Each of the superfamilies in the Neocaudata (see Table 4) exhibits a combination of primitive (with respect to the Neocaudata) and derived character states, necessitating hypotheses of derivation from a common ancestor in all cases (see Fig. 103). Plethodontids are probably structurally most like the true ancestor of the suborder, although they differ in lacking lungs and the possession of tooth plates on the parasphenoid. The family bridges the structural gap between ambystomatids and the other families of the Neocaudata.

Exact cladistic relationships of the Proteoidea to the other superfamilies are not certain, as the structural evidence is equivocal. The lack of intravertebral exits for spinal nerves and the relatively high chromosomal number (n=19) might be taken as evidence that Proteoids are the most primitive neocaudates. However, such an hypothesis necessitates assuming convergent development of such exits and the low chromosomal number (n=14 in ambystomatids, amphiumids, and plethodontids) in the other families, which is probably less likely. It is most reasonable to assume secondary development of the higher chromosomal number and lack of intravertebral exits in proteoids. Nevertheless, proteoids are here considered to be early derivatives of neocaudate stock (see Figs. 103 and 104), based on their early fossil record and autapomorphies (see above).

There is good evidence that the Plethodontoidea and Salamandroidea share a common ancestor, probably most similar to plethodontines osteologically and myologically. The relationship is indicated by the patterns of spinal nerve exits (see also Edwards 1976), the low chromosomal number (sirenids probably being tetraploid), structure of the *subvertebralis* (see Fig. 90), retention in the more primitive salamandrids of a free *rectus abdominis profundus* also found in plethodontids (see above), and the structure of the tarsus (see Schaeffer 1941). Divergent specializations are shown in the vomerine teeth, condition of the lungs, and structure of the auditory region.

What I believe to be the most accurate phylogenetic representation of the history of the Caudata is given in Figure 104. Although cladograms were utilized in analysis of the relationships of certain families, tribes, and genera, the cladistic approach has not proven useful or realistic in representing the overall phylogeny. The phylogenetic scheme is based on a variety of different characters (see above) and the characters are given differing weights from group to group. The phenetic approach was not used as there is not a sufficient number of characters that can be applied throughout the order. I do not believe that mere enumeration of features and/or cluster analysis is particularly useful for the Caudata.

The phylogenetic reconstruction is more realistic, more consistent with the phenetic and cladistic evidence, and provides a clearer visualization of the history of the Caudata than would a cladogram. Where reasonable, lineages have been shown as arising from known families, but in other cases families are shown as coming from a hypothetical common ancester. This treatment is more practical than an attempt to force all families into a rigid cladistic framework, which would both distort relationships and claim less than it is possible to claim. By the same token, cladistic classification would lead to absurd results. For example, the Neocaudata would have to be considered a subfamily of the Ambystomatidae, which is not consistent with the realities of the evolutionary history (cladistic *and* patristic) of the Caudata. The evolutionary approach also ignores the proliferation of higher taxa demanded by cladistics. The classification (Table 4) is strictly evolutionary, with both aspects of the phylogenetic process clearly taken into account, and consistent with the phylogeny that I have constructed.

C. Biogeography

Although attention has been paid to the biogeography of certain of the families of salamanders, there has been little work on historical biogeography at the familial level. Savage (1960) and Wake (1966) deal with the ranges of the plethodontids and how these might have developed historically. Steward (1969) briefly discussed the effect of Pleistocene glaciation on the salamandrids of Europe and Tihen (1958) proposed a detailed theory of dispersal in the North American ambystomatids (see also above). Various workers have discussed the data available from the fossil record and its input into biogeographical reconstruction (see Estes 1965a, 1970, Tihen 1964). Dunn (1923b) considered the distribution of amphibians in order to test the theories of dispersal put forth by Matthew (1915) and Willis (1922). He found both views at variance with the facts.

Within the Caudata, centres of origin and subsequent patterns are difficult to elucidate owing to the early origins of the families, the lack of an adequate fossil record, the presently disjunct distributions, and the difficulty of interrelating the families. Nevertheless, historical biogeography of the salamanders is not completely hopeless. It is possible to draw certain tentative conclusions that are consistent with the known evidence.

The phylogenetic relationships of the eight Recent and two fossil families are relatively well understood (see above, also Fig. 104). Present ranges, ecological tolerances, habitat preference, and preferred climates are known. There is also fairly extensive information about paleogeography of the Northern Hemisphere (see

McKenna 1972, Russell 1975, Williams and Stelck 1975), with the most critical periods of time being the Cretaceous and early Tertiary. Various methods have been proposed that purport to enable the investigator to make inferences of past centres of evolution and paths of dispersal. There are perhaps seven such techniques, all of which are based on *a priori* assumptions, but some having a much more reasonable basis than others. The major problem is how to allow adequate testing of models outside of the framework of the assumptions. Certain of these biogeographic theories are proposed as general laws, when in fact they are not even adequate generalizations about specific groups.

Before considering salamanders specifically, it is necessary to discuss the different methods available. The most recently proposed approach is that of Crozait et al. (1974), which assumes that dispersal has *not* been important in the development of present patterns of distribution. It is believed that the main process is one whereby a "generalized," primitive stock inhabiting a wide area is passively split by geographical barriers so as to give rise to new species. If this is accepted, then a simple summation of the present distributions of a monophyletic taxon will give the area occupied by the ancestral species. Observations of Recent organisms, consideration of evolutionary theory, and study of the fossil record (e.g., horses) show this method to be sterile and in major disagreement with the real evidence. Darlington (1957, p. 29) notes that it must be remembered "*that animals are living things, which are constantly evolving and multiplying in some places, spreading into other places, and dying out* *in others, and thus forming new geographical patterns.* All zoogeographers [?should] know this, but not all think about it" (italics original). "Hologenesis" does not bear serious discussion and, although Croizat et al. (1974, p. 277) speak of formulating "explicit methods of statistical analysis [based on the concept of generalized tracks] that yield unambiguous and repeatable results," Dunn (1923b, p. 136) long before noted such "excellent examples of the use of statistics in support of conclusions to which they are irrelevant."

A second technique is the numerical (see Ross 1974). This assumes that the area having the greatest diversity of Recent species is the centre of origin for that particular taxon. This is doubtless true in certain cases, but it is to be demonstrated rather than assumed. The geographic technique is quite similar, assuming that the centre of dispersal is best determined by the geographic centre of the group's present range. As in the case of the numerical method, this can be a useful piece of evidence, but is to be demonstrated in each individual case.

The ecological approach states that if the direction of dispersal is known for a certain group any taxon in more or less direct ecological association will have the same direction of dispersal. This rule is probably usually true, but it is not of general applicability and the investigator must be certain that the ecological associations are not newly evolved (see Ross 1974 for discussion of these approaches).

According to the "age and area' hypothesis of Willis (1922, see also Hennig 1966, Brundin 1972b), the present distribution of the more primitive members of a group defines the centre of origin. Although certain theoretical justifications can be made for this "rule" and it can, in some cases, be used to corroborate theories of centres of origin, it is to be demonstrated rather than accepted as a necessary truth. The biogeographic approach of Matthew (1915) and Darlington (1957, 1965) stands in direct opposition to the theory of Willis. According to Matthew, the distribution of the more derived members of a group will define the centre of origin of the group. The concept is that new, more "vigorous" species arise in an area and successively force the older, more primitive, members to the periphery. However, if we believe as seems reasonable that all species are adapted to their environments, there is no compelling reason to assume that either apomorphic or plesiomorphic species should be necessarily competitively superior. The concept, although doubtless true in certain cases, does not follow as a necessary consequence of observation or of theory.

These six methods are all based on one or more hard assumptions. Accepting the assumptions of any of these approaches and following the proper methodologies will produce answers. Unfortunately, the assumptions are not reasonable as general rules and are more likely to lead to error than to fact.

A final approach and, I would suggest, the only reasonable one is the evolutionary or phylogenetic. This method considers populations to be dynamic, evolutionary units and uses all possible lines of evidence in reconstructing past distributions and centres of origin. The evolutionary approach, like those noted above, is based on assumptions, but on assumptions that are demonstrably reasonable. It is accepted that organic evolution by means of natural selection is a reality, that living species have ancestors potentially represented in the fossil record, and that dispersal is a fact. Various tools are available to the evolutionary biogeographer, including:

1. Neobiological: descriptive zoogeography,
   ecological zoogeography,
   comparative anatomy (leading to phylogenetic conclusions).
2. Paleobiological: known first occurrences of taxa,
   paleozoogeography,
   comparative anatomy (leading to phylogenetic conclusions).
3. Geological: continental drift and plate tectonics (allowing for paleogeographical reconstructions),
   paleoclimatology.

All of these tools are absolutely essential if biogeographic research is to be meaningful and productive. If one is limited (by necessity or choice) to neobiological analysis, the answers that are produced will have a lower degree of probability. If geological data are added to the neobiological data, the probability of approximation to reality increases. However, these geological data must be real and not manufactured so as to support some special theory (e.g., one cannot raft tectonic plates merely to support some theory of vicariance).

Finally, only the fossil record can show us where animals actually existed and at what times, as opposed to where a theory might demand that they be. For example, lacking the known fossil record, who could have determined the centre of origin of the mammalian perissodactyls (rhinos, tapirs, and horses) to have been North America? Methods such as those utilizing "age and area" or "generalized tracks" are demonstrably inappropriate to situations in which centres of origin can be reasonably inferred and, therefore, especially to be avoided in situations lacking fossil data.

In attempting to elucidate the past histories of the families of salamanders it is necessary to start from what is known and proceed to what may be reasonably inferred. A brief summary of present ranges and known first occurrences is provided for each of the families:

Hynobiidae

1. Presently restricted to eastern Asia.

2. Questionably known from the Paleocene of Europe, otherwise there is no fossil record.

Cryptobranchidae

1. Disjunct distribution, two species in eastern Asia and one in eastern North America. From the fossil record and present ecological correlations it is probably to be concluded that this does not represent a relict distribution, but one of shifting ranges, moving through time as the enviornment changed.

2. First known from the Paleocene of North America (jaw material, Ravenscrag Formation, Saskatchewan), and also from the Oligocene through Pliocene of western Europe and the Miocene and Pliocene of eastern North America (Westphal 1958, Meszoely 1966).

Amphiumidae

1. Found only in the southeastern United States.

2. First known from the Upper Cretaceous and Paleocene of the western interior of North America (Estes 1969b).

Scapherpetontidae

1. Known from the Upper Cretaceous and Paleocene of the western interior of North America (Estes 1969a, 1975, 1976, Estes et al. 1969).

Ambystomatidae

1. Found throughout most of North America.

2. First known from the Paleocene (Peabody 1954) and Eocene (Estes 1965b). It is possible to refer fossils from the Oligocene and Miocene of North America to extant species groups (see above).

Batrachosauroididae

1. Known from the Upper Cretaceous through to the Miocene in the western interior and southeastern parts of North America (see Estes 1969a, Naylor 1978a), and probably from the Paleocene and Eocene of western Europe (Herre 1935b, Estes et al. 1967, Naylor 1978a).

Proteidae

1. Found in the Appalachians of eastern North America and in western Yugoslavia.

2. First found in the Paleocene of Saskatchewan (Naylor 1978b), and also from the Oligocene of North America (Estes pers. comm.) and the Miocene of the Caucasus (Estes and Darevsky 1977).

Plethodontidae

1. Found in eastern and western North America, Central America, northern South America, and western Europe.

2. The fossil record is all but nonexistent, the family being first recorded by Pliocene trackways of *Batrachoseps* in California.

Salamandridae

1. Found in eastern and western North America, throughout Europe and in eastern Asia, as well as in the Middle East and northern Africa.

2. First known from the Paleocene of Europe (see Estes et al. 1967), then from the Oligocene and Miocene of North America and the Miocene of eastern Asia (Tihen 1974, Young 1965).

Sirenidae

1. Found in the southeastern United States.

2. Known first in the Upper Cretaceous of the western interior of North America (Estes 1964), with specimens referable to extant genera appearing in the early Tertiary of the same continent (Goin and Auffenberg 1955, 1957).

To this evidence must be added what has been reconstructed of the paleogeography of Cretaceous and early Tertiary time. Four areas are of importance in this regard: the De Geer land bridge connecting North America and Europe, the Turgai Straits separating Asia from Europe, the western interior seaway of North America, and Beringia (see Fig. 105). The De Geer land bridge allowed faunal exchange between Europe and North America until the middle Eocene, when the Atlantic Ocean disrupted it (McKenna 1972, Russell 1975). The Turgai Straits were present through almost all of the Cretaceous (Lillegraven 1974), allowed intermittent passage (at least of mammals) in the Paleocene and early Eocene, were fully developed by the middle Eocene, and then closed at the end of the Eocene to allow dispersal between Europe and Asia (Russell 1975). The area of Beringia was split by the Arctic and Pacific oceans in the Late Jurassic and into Neocomian (Early Cretaceous) time. Thereafter Beringia served as an intermittent filter route for dispersal between Asia and North America (Lillegraven 1974, Russell 1975). Based on the fossil evidence and inference from the living families, it is likely that the Cretaceous and early Tertiary saw the development of the living groups of salamanders and their dispersal to the present ranges (see Tihen 1958, Estes 1965b, 1970).

In addition to this evidence, it is now possible to provide a reasonable phylogenetic scheme for all of the families of living salamanders (see above, also Fig. 104). These data together allow for the development of the following tentative proposal (see Fig. 105).

The Hynobiidae are the most primitive group of living salamanders, probably representative of the truly ancestral salamanders. If the Paleocene (*Wolterstorffiella* and *Geyeriella*) and Miocene (*Bargmannia*) fossils from Europe are correctly interpreted as hynobiids, the distribution of hynobiids was previously more extensive. Cryptobranchids, their closest living relatives, may have entered North America some time prior to the Tertiary, where they are represented by jaws from the Paleocene Ravenscrag Formation of Saskatchewan. Subsequently, the family is represented by specimens from the middle Tertiary of Europe and North America. Whether or not cryptobranchids originated in North America is uncertain, however. The European *Cryptobranchus scheuchzeri* is at least structurally ancestral to the east Asian *C. japonicus*, perhaps indicating dispersal westward across the area of the old Turgai Straits after the Eocene (see Westphal 1958). *C. alleganiensis* appears to be a relatively recent, paedomorphic derivative from a similar stock. Although the present distribution of cryptobranchids could be interpreted as relict, it is more probable that this represents the end result of a history of shifting ranges and dispersal.

The Ambystomatoidea are probably a monophyletic stock (sensu Simpson 1961) derived from hynobiid ancestors that entered North America from Asia sometime in the Cretaceous, although this could perhaps be interpreted as a vicariance event from hynobiid stock already present in North America. The resultant pro-ambystomatids gave rise to amphiumids and scapherpetontids, these latter families being known from Late Cretaceous deposits from the old western shore of the interior seaway. Amphiumids managed subsequently to establish themselves in the southeast of the United States, but scapherpetontids went extinct. Meanwhile, the ambystomatids were evolving, with dicamptodontines segregating to the west of the Rocky Mountains and ambystomatines spreading more widely. The presence of the more primitive ambystomatids (*Dicamptodon*, *Rhyacotriton*, *Ambystomichnus*, *Ambystoma gracile*, *A. macrodactylum*, and *A. tiheni*) in western North America may indicate this to have been the centre of origin of the Ambystomatidae. More derived ambystomatines diverged from the older stock, perhaps in Appalachia, where the *Ambystoma maculatum* group is centred, as well as the more derived members of the genus. Dispersal into Mexico was probably the last event in the origin of the present distribution of the ambystomatines.

It is likely that the Ambystomatoidea have always been restricted to North America, where they gave rise to the neocaudate salamanders, which came to be more widely dispersed. If, as seems likely, the Neocaudata are a monophyletic group of ambystomatoid ancestry, it is probable that these more derived salamanders originated in North America. The most structurally primitive neocaudates (plethodontids) are centred in North America, and the Batrachosauroididae are known from Upper Cretaceous deposits in the western interior of the same continent. Plethodontids probably arose from ancestors that, if known, would be readily classified as Ambystomatidae. Based on the present distribution of the most structurally primitive tribe, the Plethodontini, it would seem that the family was originally widely spread over North America. A major adaptive radiation resulted in both eastern and western North America: in the east the Euryciini evolved, eventually giving rise to the Desmognathini, while in the west the Bolitoglossini diverged and gave rise to representatives that eventually reached Europe (probably via Beringia) and also South America. The dating of these events is most uncertain, perhaps being Late Cretaceous or early Tertiary.

It is likely that the Salamandridae share a common ancestor with the Plethodontidae (see above), but the place of origin of the salamandrids is uncertain. The salamandrid radiation centred in Europe, which contains the most primitive living genera (within the Salamandrinae and Pleurodelini) and the earliest and most extensive fossil record of the family (see above, also Kuhn 1962, Estes et al. 1967, Estes and Hoffstetter 1976). From the European centre, it is likely that the Asian newts of the *Cynops* group, as well as the more primitive *Tylototriton*, dispersed eastwards after the closing of the

Turgai Straits in the Eocene. The first known fossil newt (*Procynops*) from eastern Asia is of Miocene age (Young 1965), and *Tylototriton* and allied genera are known from the middle Tertiary of Europe (see above).

The North American newts perhaps entered via the De Geer land bridge prior to the middle Eocene, where they split into the two extant genera. These are known from the Oligocene and Miocene of North America (see Tihen 1974). On the other hand, if the *Notophthalmus* group is diphyletic, *Taricha* may have entered North America from Asia through Beringia.

As argued above (see also Fig. 104), it is likely that proteoids are relatively early derivatives from neocaudate stock. Batrachosauroidids are known from the Upper Cretaceous of the interior of North America, and the first proteids come from the Paleocene of Saskatchewan (Estes 1964, Naylor 1978a,b). The deltaic lowlands along the eastern shores of the western interior seaway (Estes et al. 1969, Estes and Berberian 1970) would have provided ideal habitats for the aquatic, larval representatives of these two families. Batrachosauroidids are also known from the Miocene of southern and southeastern North America (Estes 1969a), and the European representative of the family, *Palaeoproteus*, may have entered Europe via the De Geer bridge in the early Paleocene.

The Proteidae probably originated in North America, dispersing subsequently into Europe where they are presently represented by *Proteus*. It is probably not reasonable to call the present distribution of proteids relictual. Rather it is owing to a shifting of ranges and continuous dispersal. If proteids are as close to batrachosauroidids as is here argued (see above), they probably originated some time in the latest Cretaceous or earliest Paleocene directly from the Batrachosauroididae.

The final family, the Sirenidae, has probably always been exclusively North American. The earliest representative of the family, *Habrosaurus*, from the Upper Cretaceous of the western interior of North America (Estes 1964, 1976) is extremely derived, thereby indicating an earlier origin for the family. If, as seems likely, sirenids originated from within the Salamandridae, this would place the origin of the latter considerably prior to the beginning of the Tertiary. Sirenids may well have originated along the western interior seaway of North America, dispersing eastwards as the oceans retreated after the end of the Cretaceous.

SUMMARY

1. The vertebral columns of representatives from each of the living families, including 18 species in 14 genera, are described in order to present the basic structural plans of each family. The descriptions are of the atlas, second cervical, a mid-trunk vertebra, the sacrum, and a haemal vertebra. Variation along the column of condyles and/or cotyles, hypapophyseal structures, neural arches, zygapophyses, and transverse processes are also provided. These raw data relate to:

   i) interpretation of the fossil record,
   ii) myological investigation of the trunk region,
   iii) phylogenetic interpretations of the order.

2. Detailed descriptions and figures of the axial musculature in the midtrunk region of representatives from all of the extant families, including 61 species in 37 genera, are provided. This documents a major amount of diversity and interfamilial variation in all portions of the axial musculature.

3. Studies of the vertebrae and trunk musculature demonstrate that certain features observed on fossil vertebrae are of important taxonomic significance. These include: aliform processes, anterior basapophyses, and posterior basapophyses. Other features are of more minor importance.

4. Dissections of the trunk musculature of salamanders, as well as of certain snakes and lizards, allow for the proposal of more detailed

hypotheses on the origin and significance of the ball-and-socket intercentral joint. This joint serves primarily as a strengthening device, preventing dislocation of the intercentral joints.

5. Amphicoelous salamanders are aquatic, of small size, possessed of larger amounts of trunk musculature distal to the column, and/or possessed of complex flexures that concentrate force away from the column. These factors indicate reduced strain intercentrally.

6. Opisthocoelous salamanders have a more intimate association of musculature with the vertebrae and have reduced the complexity of the *subvertebralis* and (to a lesser extent) the *dorsalis trunci*. This produces increased intercentral strain.

7. The majority of opisthocoelous salamanders do not have a true ball-and-socket joint. The joints are cup-in-cup, clearly indicating the anti-dislocation function (see Fig. 93) and that the joint is not primarily serving to increase flexibility.

8. The end of the centrum developing the "ball" depends on Fick's rule. If the pull is posterior and concentrated on the rear cotyle, then opisthocoely develops (plethodontids, batrachosauroidids, and salamandrids). If the pull is anterior and on the forward cotyle, then procoely develops (snakes and lizards).

9. Elongate transverse processes are hypothesized to be owing to two factors:

i) they are possible owing to the buccal pump method of lung ventilation,

ii) they are present because they serve as rigid parts of the myosepta, being points of attachment for intervertebral muscle fibers, probably owing to the necessity for the rapid initiation of locomotion in prey capture and predator escape.

10. Bicipital rib-bearers do not develop in order to counteract the pull of gravity on the viscera (compare lizards and frogs), but because of locomotory constraints. The rib-bearers and ribs are integral parts of the myoseptal system.

11. A discussion of biological systematics is provided, in which it is concluded that:

i) the study of function is necessary in phylogenetic analysis,

ii) the premises of both phenetic and cladistic approaches to taxonomy and phylogenetic analysis are to be rejected,

iii) the evolutionary approach to systematics is accepted as the most reasonable.

12. A series of principles to be used in phylogenetic analysis are proposed, what constitutes "good" phylogenetic characters is considered, and concepts pertinent to systematic study are discussed (i.e., homology, parsimony, primitiveness, and the biogenetic "law").

13. A series of principles to be used in biological classification is

provided and defended. Evolutionary classification is accepted as the most reasonable approach to ordering the organisms.

14. A brief history of concepts of classification of salamanders since the time of Linnaeus is provided, in order to show the historical development of present ideas and to illustrate the necessary subjective component in classification. Classification is partly science and partly art, by necessity.

15. Hynobiids and cryptobranchids are accepted as closely related, representative of the most primitive living salamanders, and to be classified in the superfamily Cryptobranchoidea.

16. Primitive characters retained by hynobiids include: paired premaxillae with short nasal spines, retention of lacrimal and septomaxillary, retention of angular and prearticular in lower jaw, columella and operculum in middle ear, external fertilization, retention of second epibranchials in the adult hyobranchium, relatively long and low vertebrae, centra amphicoelous, appressed rib-bearers, postatlantal spinal nerves exiting intervertebrally, *subvertebralis* with anterior basapophyseal musculature and associated transverse process flexures, *rectus abdominus* divided into the *r. a. superficialis* and a free *r. a. profundus*, and only two layers of lateral abdominal musculature in most metamorphosed adults.

17. Scapherpetontids, amphiumids, and ambystomatids are to be grouped in the superfamily Ambystomatoidea, which evolved from hynobiid or

hynobiid-like ancestry. The superfamily is united by a series of characters: internal fertilization by means of a spermatophore (where known); fusion of angular and prearticular; some, but not all, post-atlantal spinal nerves exiting intravertebrally; and retention of the primitive sort of trunk musculature.

18. *Rhyacotriton* and *Dicamptodon* are grouped into a single subfamily, the Dicamptodontinae, as sharing unique features, both primitive and derived with respect to ambystomatines. These include: separate prootic, foetalized trunk vertebrae, pattern of exits of spinal nerves, structure of the *dorsalis trunci*, and structure of the lateral abdominal musculature.

19. The following modification to Tihen's (1958) species groups of the genus *Ambystoma* are suggested:

i) *A. macrodactylum*, *A. gracile*, and probably *A. tiheni* are placed in a new species group, as being the most primitive *Ambystoma*, perhaps inhabiting the ancestral area of the Ambystomatinae.

ii) The *A. tigrinum* species group is held to also include Tihen's *A. mexicanum* species group and the subgenus *Bathysiredon*.

iii) Continued usage of the subgenera *Ambystoma* and *Linguaelapsus* is rejected, the latter becoming the *A. cingulatum* species group.

iv) The *A. tigrinum* complex of species is the most highly derived (paedomorphic) of the genus *Ambystoma*.

v) The *A. maculatum* species group is derived from the *A. macrodactylum* group and, in turn, gave rise to the *A. opacum*, *A. cingulatum*, and *A. tigrinum* species groups.

vi) *Rhyacosiredon* is the most derived member of the Ambystomatidae, being derived via paedomorphosis from the *A. tigrinum* group.

20. Derivation of plethodontids from ambystomatid ancestry is accepted, but an argument for close relationship to the salamandrids is also made, the two families probably sharing a "sister-group" relationship. This is indicated by the pattern of spinal nerve exits, the structure of the *subvertebralis* and lateral abdominal musculature, the structure of the tarsus, and the development of the premaxillae.

21. It is tentatively suggested that the most primitive pattern of reproduction within the Plethodontidae is that seen in the Plethodontinae, which lay terrestrial eggs and generally brood them. This means that the aquatic larval stage of the Desmognathinae is secondary, as is all but certainly the case in *Hemidactylium*.

22. *Hemidactylium* and *Batrachoseps* are included in the tribe Plethodontini, along with *Plethodon*, *Aneides*, and *Ensatina*. The Bolitoglossini then includes *Hydromantes* and the supergenus *Bolitoglossa*. These two tribes have a sister-group relationship and are classified in the subfamily Plethodontinae.

23. Wake's (1966) Hemidactyliini is here termed the Euryciini, owing to removal of *Hemidactylium*. A tribe Desmognathini is recognized to

include *Desmognathus*, *Leurognathus*, and *Phaeognathus*. These two tribes share a sister-group relationship and are included in the Desmognathinae, which shares a common ancestry with the Plethodontinae.

24. Continued recognition of *Leurognathus* as a genus distinct from *Desmognathus* is questioned, but no formal taxonomic change is proposed.

25. Close relationship of *Proteus* and *Necturus* is justified, the arguments of Hecht and Edwards (1976) being considered, but not accepted. Proteids also share a derived condition of the *subvertebralis*, which further justifies an hypothesis of monophyly.

26. Proteids and batrachosauroidids are considered to be closely related and to be properly classified in the superfamily Proteoidea. Estes' (1975) suggestions are, therefore, accepted and further supporting evidence is proposed. The two families may even form an ancestor-descendant relationship.

27. Proteoids are most closely related to plethodontoids and salamandroids, being probably derived from the primitive stock that gave rise to these two latter groups. Under this interpretation the absence of postatlantal spinal nerve foramina and the high chromosomal number are secondary features.

28. Salamandrids are descended from an ancestor shared with plethodontids and, in turn, gave rise to sirenids. Evidence for this comes

from spinal nerve patterns, chromosomal numbers (sirenids being tetraploid), trunk musculature, vertebral structure, and the middle ear.

29. Sirenids and salamandrids are included in a superfamily Salamandroidea.

30. Two subfamilies are recognized within the Salamandridae: the Salamandrinae for the more primitive *Salamandra* and *Chioglossa* and the derived Pleurodelinae for the newts. The latter is further subdivided into two tribes: the more primitive Pleurodelini for *Pleurodeles*, *Tylototriton*, and *Salamandrina* and the derived Triturini for the remainder of the newts. Within the Triturini are recognized the following generic groups: the *Notophthalmus* group (*Notophthalmus* and *Taricha*), the *Cynops* group (*Cynops*, *Paramesotriton*, *Hypselotriton*, and *Pachytriton*), the *Triturus* group (*Triturus* and *Neurergus*), and the *Euproctus* group (only *Euproctus*).

31. The frontosquamosal arch and its associated cranial structures are almost certainly derived within the Salamandridae, although they are primitive within the Pleurodelinae, some of which have secondarily reduced the arch.

32. Salamandrines are primitive with respect to trunk musculature, cranial anatomy, and courtship behavior.

33. The Pleurodelini are primitive with respect to courtship, the structure of the *rectus abdominus* in *Tylototriton* and *Salamandrina*, and in laying eggs in water, but derived with respect to salamandrines in cranial structure, vertebral structure, structure of the ribs, and in the trunk musculature, notably as regards the *subvertebralis*.

34. The Caudata are divided into two suborders: the primitive anterior basapophyseal, and amphicoelous Archaeocaudata (cryptobranchoids and ambystomatoids), and the derived, posterior basapophyseal/opisthocoelous Neocaudata (proteoids, plethodontoids, and salamandroids).

35. A tentative biogeographic reconstruction is proposed:

i) Ambystomatids originated in and have probably never left North America. They find their ancestry in hynobiid or pro-hynobiid stock that entered North America well before the start of the Tertiary.

ii) Scapherpetontids and amphiumids originated from primitive ambystomatid ancestors that are represented today by dicamptodontines. They may have originated on the shores of the Cretaceous midcontinental sea, where they are represented by Cretaceous and early Tertiary fossils.

iii) Neocaudates originated in North America from ambystomatid or ambystomatid-like ancestry. None of the living families is closely representative of the early neocaudate group.

iv) Proteoids probably originated in North America from this early Neocaudate group, but with subsequent early dispersal into Europe (*Palaeoproteus*, *Proteus*, and *Mioproteus*).

v) The place of origin of salamandrids is uncertain. The oldest fossils and present centre of diversity are in Europe. If this reflects the true centre of origin, dispersal subsequently took place into Asia and North America.

vi) Sirenids probably arose from salamandrids in North America in the later part of the Cretaceous, perhaps along the shores of the interior seaway. The deltaic lowlands of this sea also seem to have seen the origin of amphiumids, scapherpetontids, batrachosauroidids, and (perhaps) proteids.

vii) The paedogenic North American salamanders (sirenids, amphiumids, and proteids) then dispersed eastward as the midcontinental sea retreated with the start of the Tertiary.

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TABLES

Table 1. Proposed classification of the family Ambystomatidae.

- Family Ambystomatidae Hallowell 1857
  - Subfamily Dicamptodontinae Tihen 1958
    - Content: *Dicamptodon**, *Rhyacotriton**, ?*Ambystomichnus*.
  - Subfamily Ambystomatinae Hallowell 1857
    - Genus *Ambystoma* Tschudi 1838
      - *A. macrodactylum* species group
        - Content: *A. macrodactylum**, *A. gracile**, ?*A. tiheni**.
      - *A. maculatum* species group
        - Content: *A. maculatum**, *A. jeffersonianum**, *A. laterale*, *A. tremblayi*, *A. platineum*.
      - *A. opacum* species group
        - Content: *A. opacum**, *A. talpoideum**.
      - *A. cingulatum* species group
        - Content: subgenus *Linguaelapsus* of Tihen (1958); *A. cingulatum* available.
      - *A. tigrinum* species group
        - Content: *A. mexicanum* species group, *A. tigrinum* species group, and subgenus *Bathysiredon* of Tihen (1958), *A. tigrinum* available.
    - Genus *Rhyacosiredon* Dunn 1928
      - Content: as Tihen (1958).

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*Available for study.

Table 2. Proposed classification of the family Plethodontidae.

Family Plethodontidae Gray 1850

  Subfamily Plethodontinae Boulenger 1882
    Tribe Plethodontini Wake 1966
      Content: *Plethodon**, *Ensatina**, *Aneides**, *Hemidactylium**, *Batrachoseps**.
    Tribe Bolitoglossini Wake 1966
      Content: *Bolitoglossa**, *Hydromantes**, *Lineatriton*, *Thorius*, *Pseudoeurycea**, *Chiropterotriton**, *Oedipina*, *Parvimolge*.

  Subfamily Desmognathinae Boulenger 1882
    Tribe Euryciini Wake & Lombard 1973
      Content: *Eurycea**, *Gyrinophilus**, *Pseudotriton**, *Stereochilus**, *Haideotriton*, *Typhlotriton**, *Typhlomolge*.
    Tribe Desmognathini nov.
      Content: *Desmognathus**, *Leurognathus**, *Phaeognathus*.

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*Available for study.

Table 3. Proposed classification of the family Salamandridae, fossil taxa not included.

Family Salamandridae Gray 1825
  Subfamily Salamandrinae Tschudi 1838
    Content: *Salamandra**, *Chioglossa*.
  Subfamily Pleurodelinae nov.
    Tribe Pleurodelini Bonaparte 1838
      Content: *Pleurodeles**, *Tylototriton**, *Salamandrina**.
    Tribe Triturini nov.
      Notophthalmus group
        Content: *Notophthalmus**, *Taricha**.
      Cynops group
        Content: *Cynops**, *Paramesotriton**, *Hypselotriton*
        Pachytriton.
      Triturus group
        Content: *Triturus**, *Neurergus*.
      Euproctus group
        Content: *Euproctus**.

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*Available for study.

Table 4. Proposed classification of the order Caudata.

- Order Caudata Oppel 1811
  - Suborder Archaeocaudata nov.
    - Superfamily Cryptobranchoidea Fitzinger 1826
      - Family Hynobiidae Cope 1860
      - Family Cryptobranchidae Cope 1889
    - Superfamily Ambystomatoidea Noble 1931
      - Family Scapherpetontidae Auffenberg & Goin 1959
      - Family Amphiumidae Gray 1825
      - Family Ambystomatidae Hallowell 1857
        - Subfamily Dicamptodontinae Tihen 1958
        - Subfamily Ambystomatinae Hallowell 1957
    - ?Archaeocaudata *incertae sedis*
      - Family Prosirenidae Estes 1969
  - Suborder Neocaudata nov.
    - Superfamily Proteoidea Muller 1831
      - Family Batrachosauroididae Auffenberg 1958
      - Family Proteidae Hogg 1838
    - Superfamily Plethodontoidea Smith & Taylor 1948
      - Family Plethodontidae Gray 1850
        - Subfamily Plethodontinae Boulenger 1882
          - Tribe Plethodontini Wake 1966
          - Tribe Bolitoglossini Wake 1966
        - Subfamily Desmognathinae Boulenger 1882
          - Tribe Euryciini Wake & Lombard 1973
          - Tribe Desmognathini nov.
    - Superfamily Salamandroidea Fitzinger 1826
      - Family Salamandridae Gray 1825
        - Subfamily Salamandrinae Tschudi 1838
        - Subfamily Pleurodelinae nov.
          - Tribe Pleurodelini Bonaparte 1838
          - Tribe Triturini nov.
      - Family Sirenidae Gray 1825

FIGURES

Figure 1. Vertebrae of selected species of salamanders, showing features and terminology discussed in the text: (A) *Necturus maculosus*, dorsal view; (B) *Desmognathus fuscus*, lateral view; (C) *Amphiuma tridactylium*, ventral view; (D) *Siren lacertina*, dorsal view; (E) same, lateralview; (F) *Amphiuma tridactylium*, posterior view. Abbreviations explained on pp. 4-7.

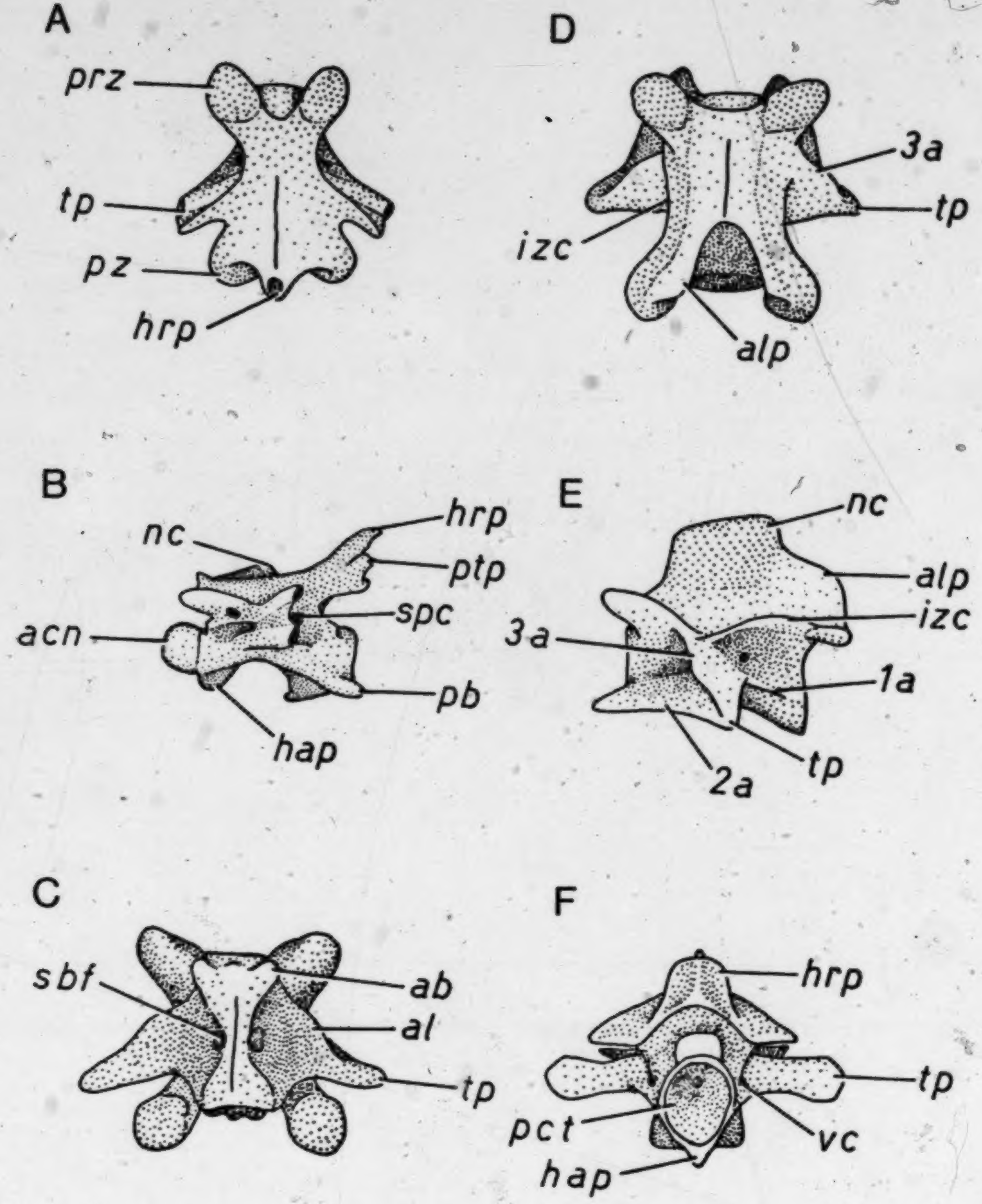
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Figure 2. Midtrunk vertebrae of hynobiid salamanders in dorsal, ventral, and lateral views: (A) *Pachypalaminus boulengeri*, T8; (B) *Onychodactylus japonicus*, T9; scale represents one millimeter.

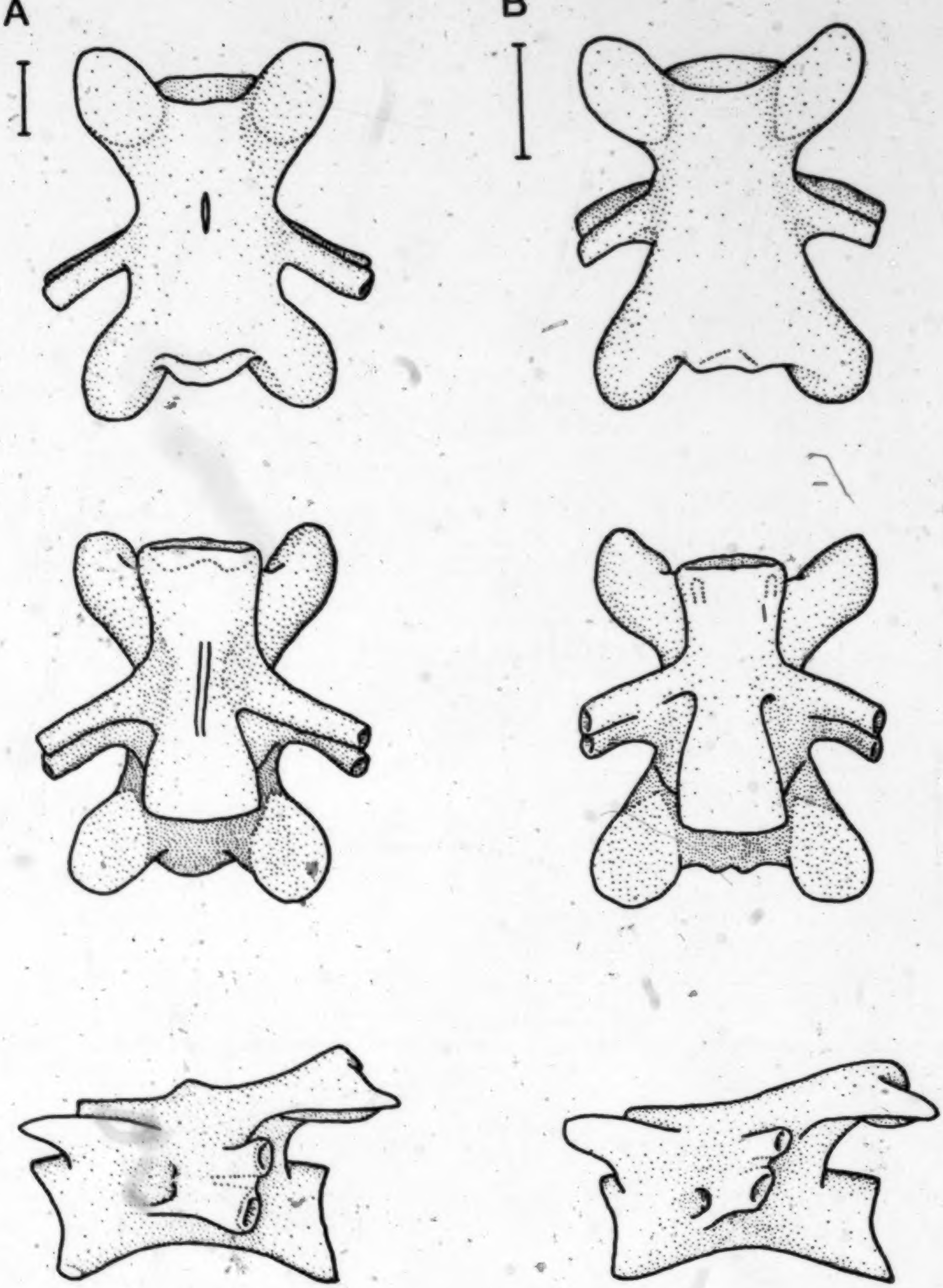
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Figure 3. Midtrunk vertebrae of cryptobranchoid salamanders in dorsal, ventral, and lateral views: (A) *Hynobius naevius*, T8; (B) *Cryptobranchus alleganiensis*, T9; scale represents one millimeter.

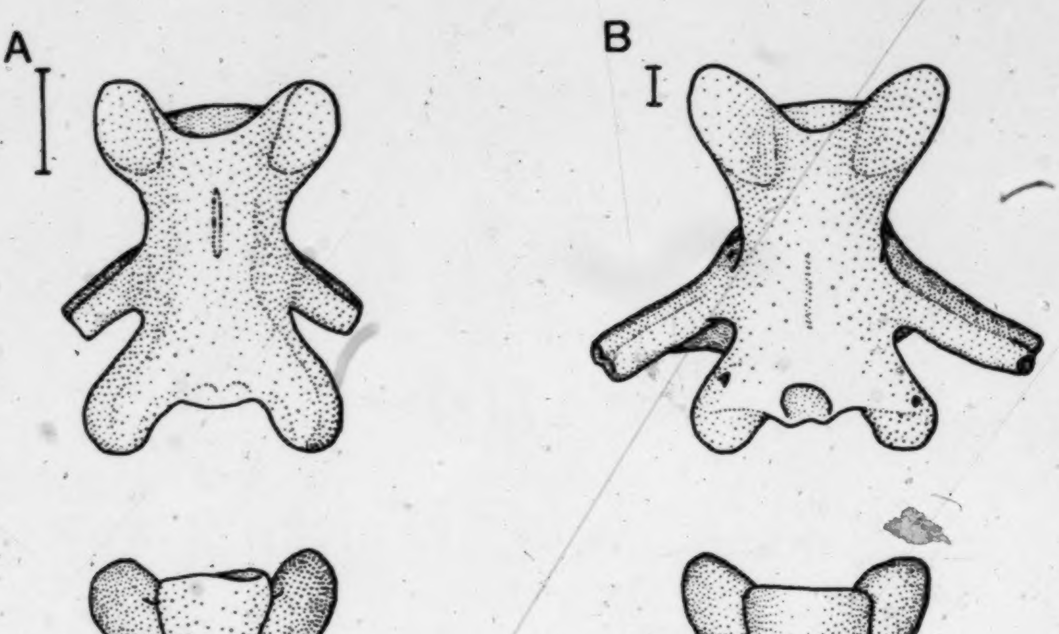
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Figure 4. Midtrunk vertebra of *Amphiuma tridactylium* in dorsal, ventral, and lateral views; scale represents one millimeter.

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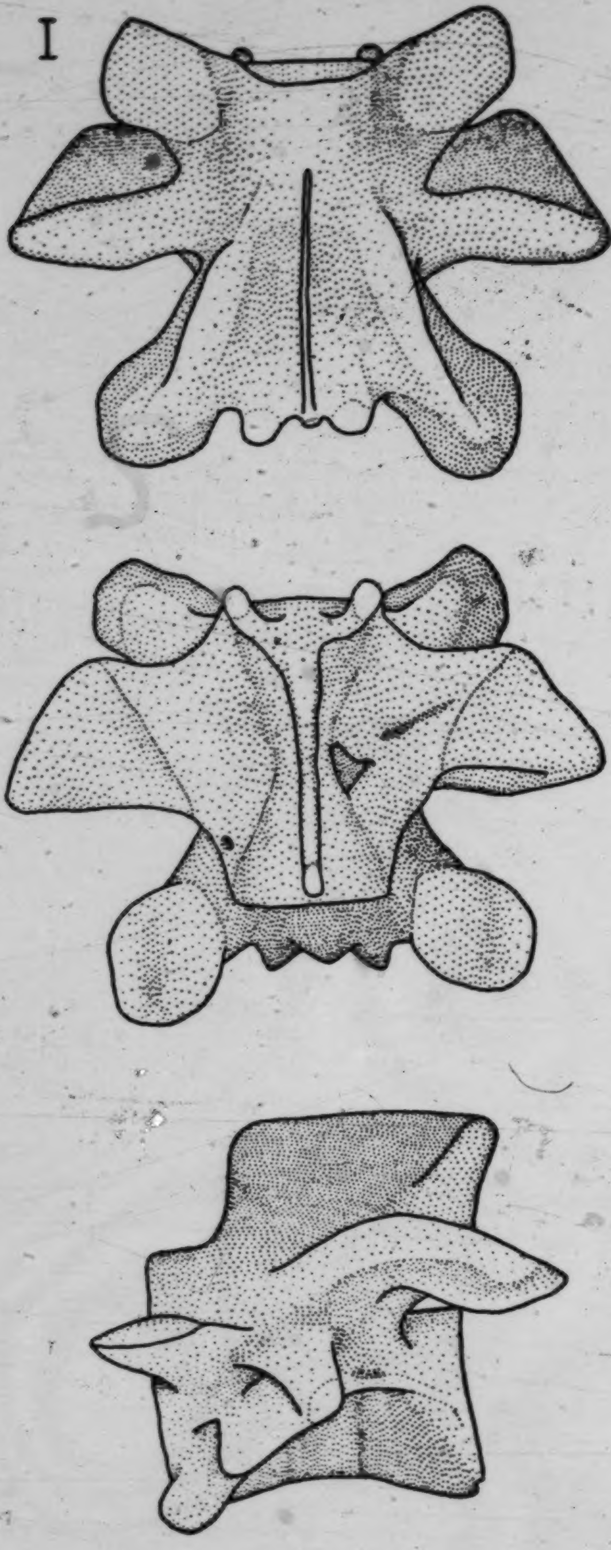
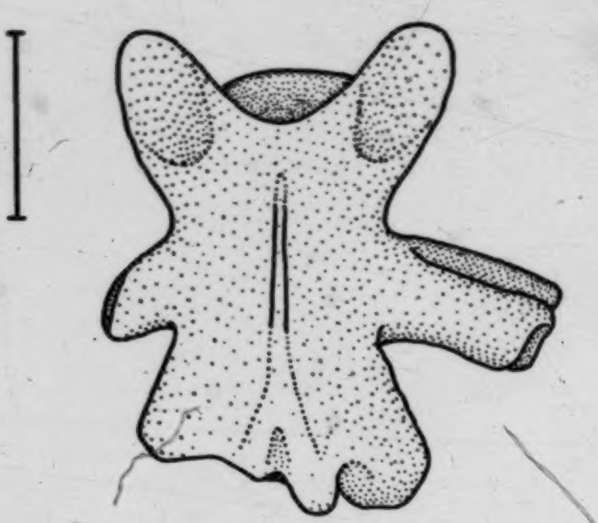
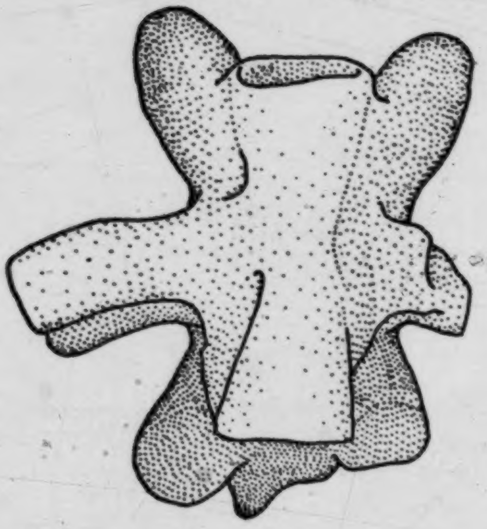


Figure 5. Trunk vertebra of *Ambystoma tiheni* (SMNH 1431) in dorsal, ventral, and lateral views; from the Oligocene of southern Saskatchewan; scale represents one millimeter.





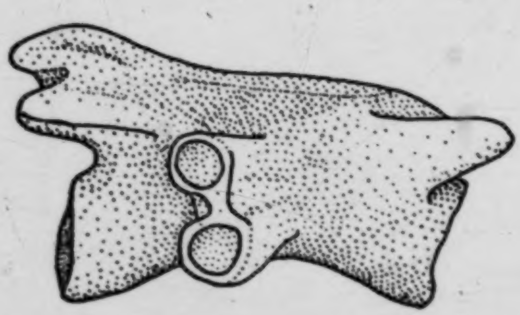


Figure 6. Midtrunk vertebrae of ambystomatid salamanders in dorsal, ventral, and lateral views; (A) *Ambystoma maculatum*, T8; (B) *Ambystoma jeffersonianum*, T8; scale represents one millimeter.

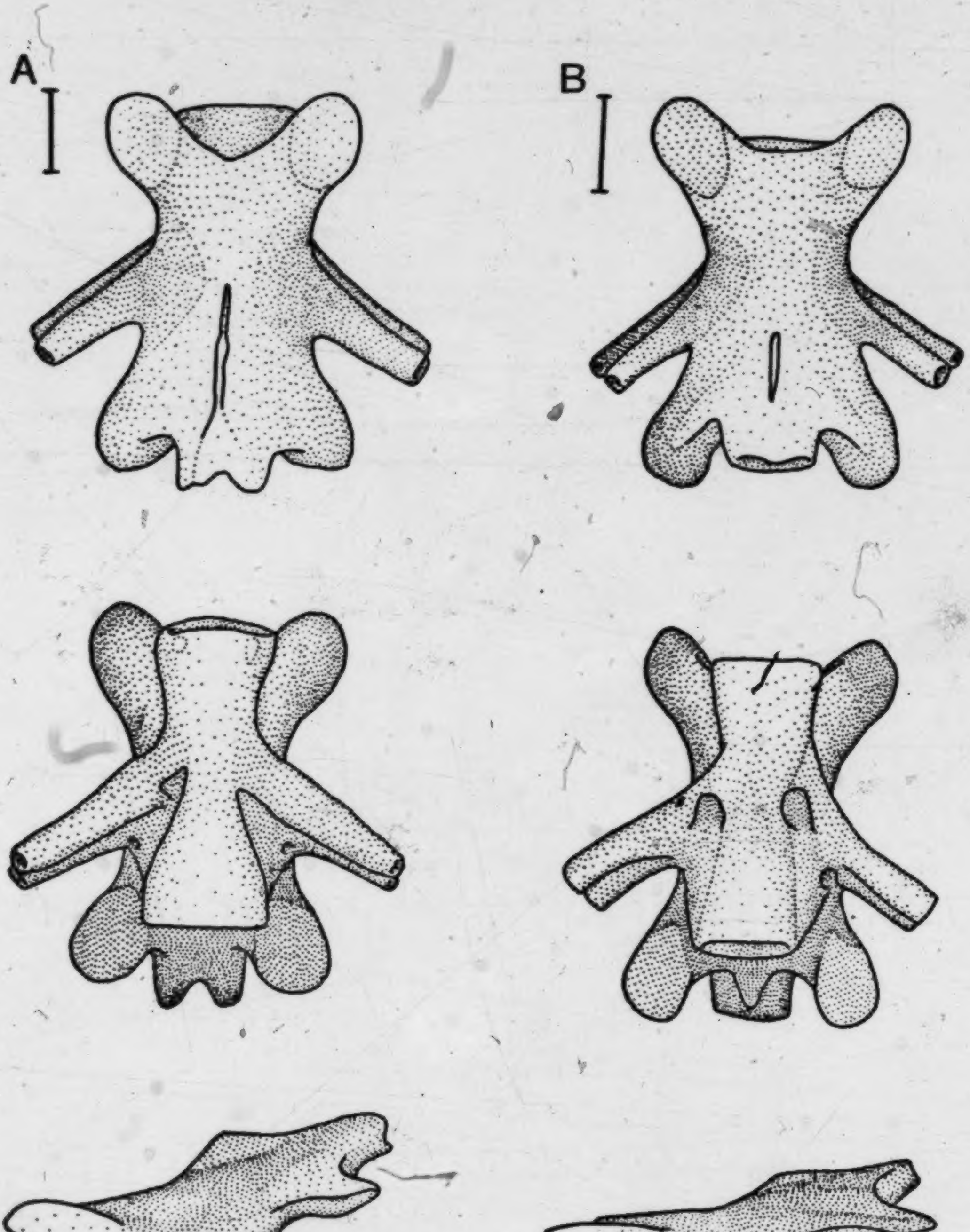

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Figure 7. Midtrunk vertebrae of ambystomatid salamanders in dorsal, ventral, and lateral views: (A) *Ambystoma gracile*, T8; (B) *Ambystoma talpoideum*, T8; scale represents one millimeter.

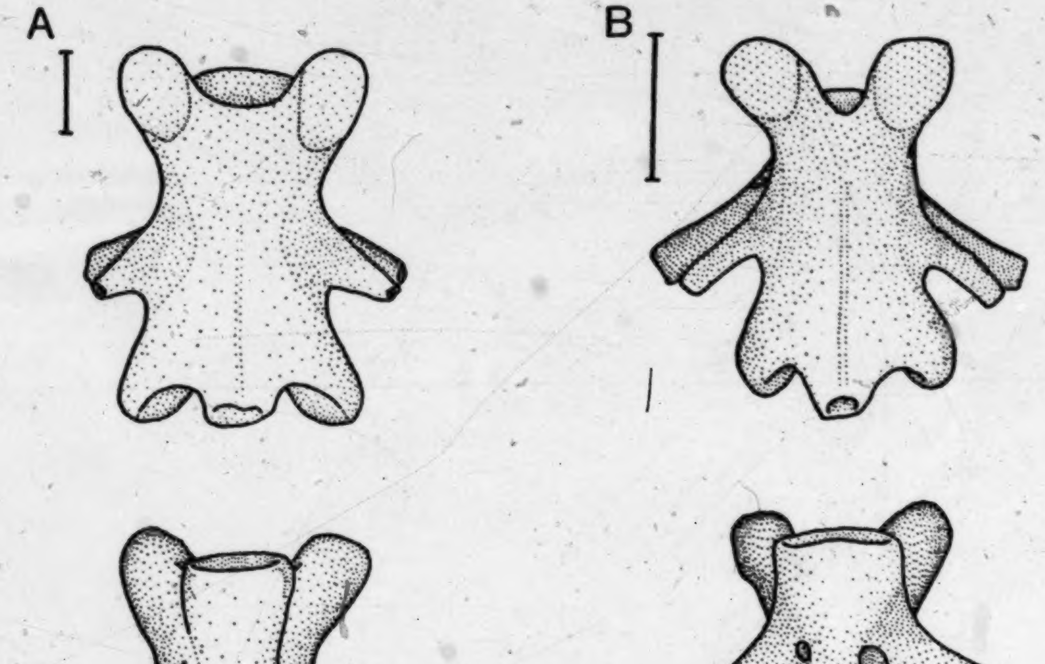
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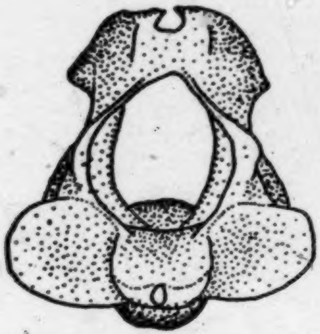
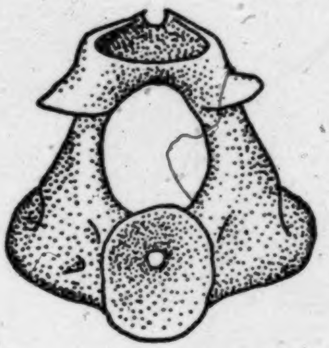
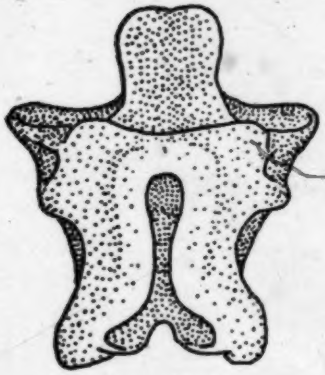
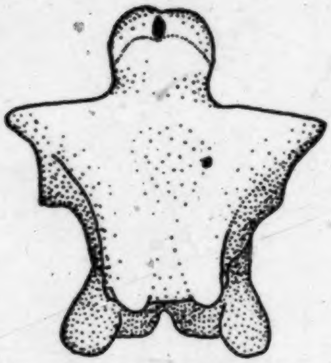
Figure 8. Atlas of young, postmetamorphic *Ambystoma tigrinum* in anterior, posterior, dorsal, ventral, and lateral views; scale represents one millimeter.









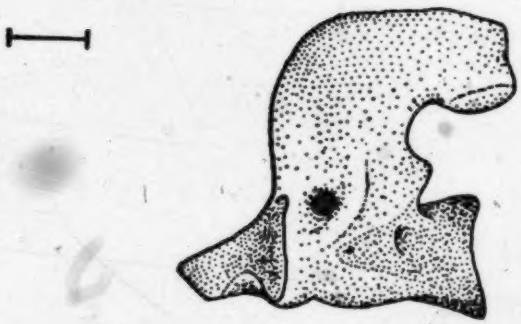


Figure 9. Midtrunk vertebrae of *Ambystoma tigrinum* in dorsal, ventral, and lateral views: (A) large metamorphosed *Ambystoma tigrinum diaboli*, T8; (B) small metamorphosed *Ambystoma tigrinum melanostictum*, T8; (C) neotenic individual of the same subspecies, T8; scale represents one millimeter.

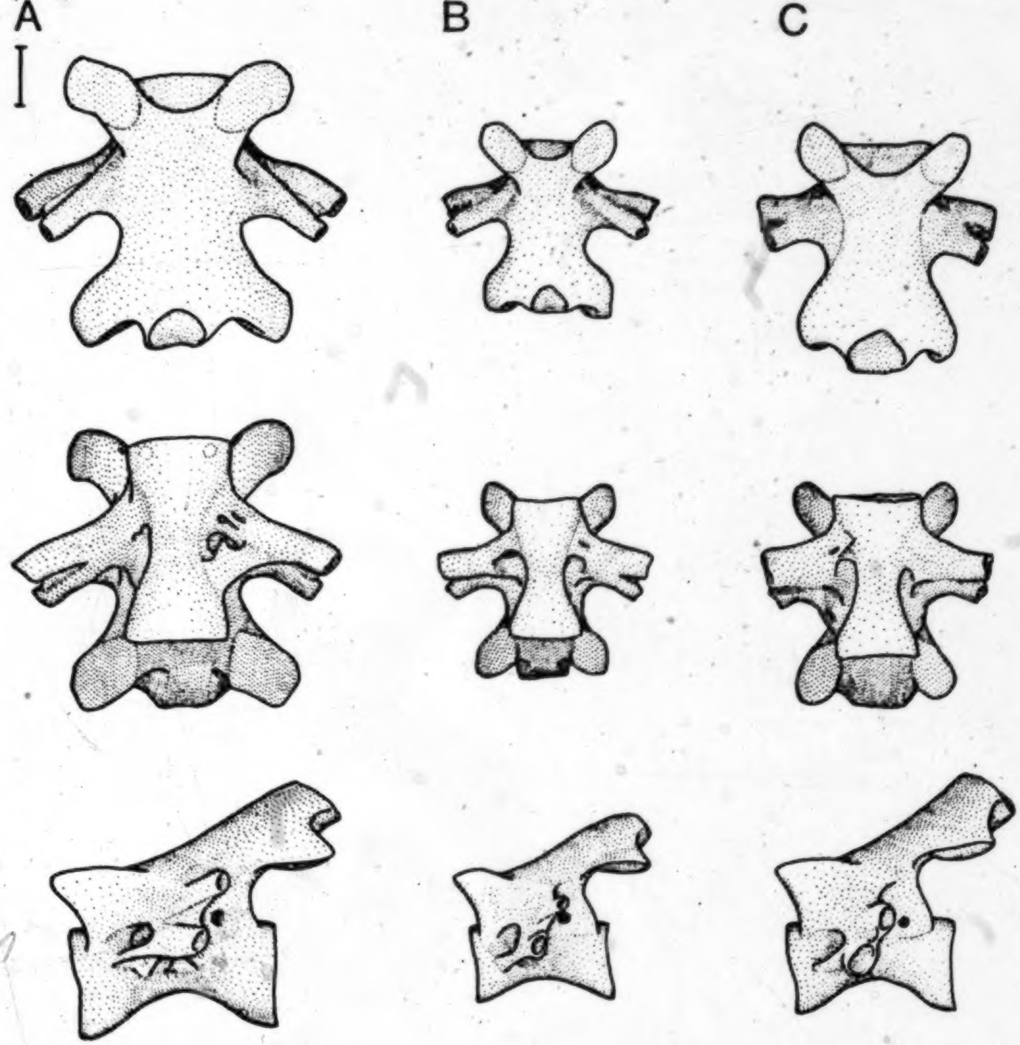

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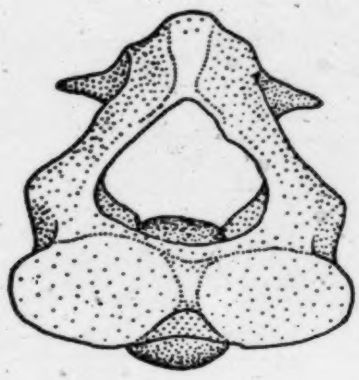
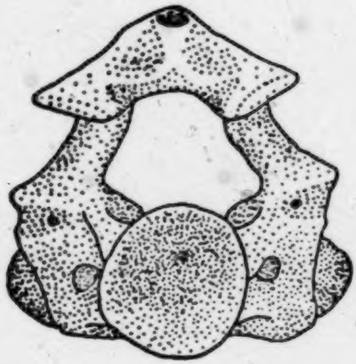
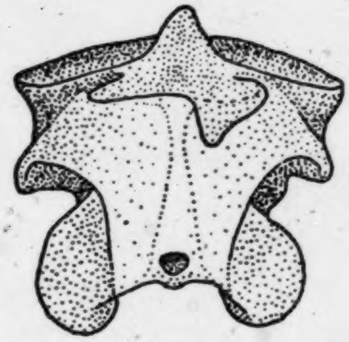
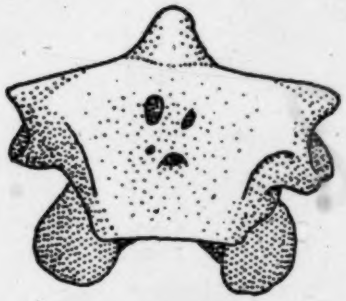
Figure 10. Atlas of *Necturus maculosus* in anterior, posterior, dorsal, ventral, and lateral views; scale represents two millimeters.









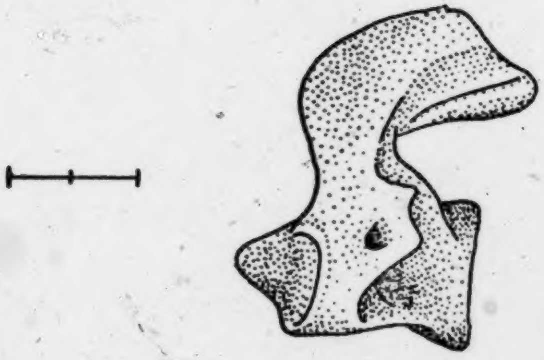
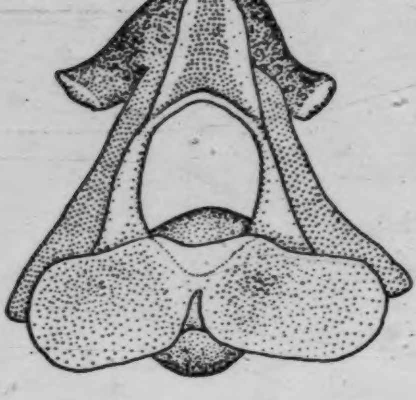
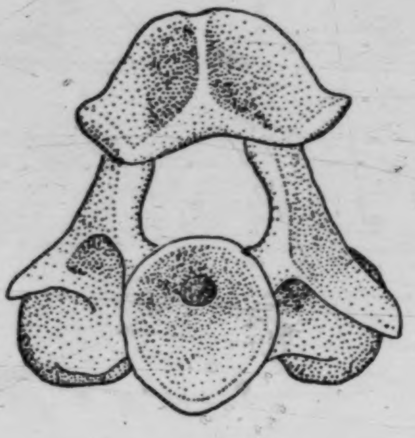
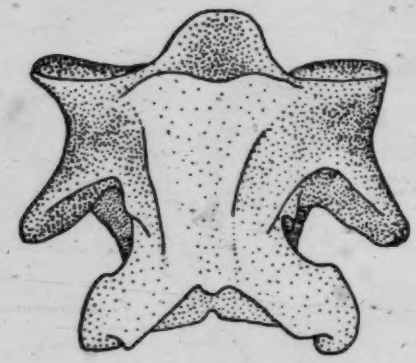
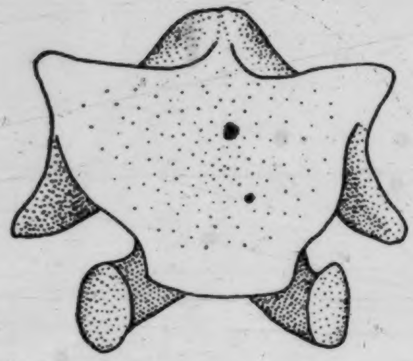


Figure 11. Atlas of *Siren lacertina* in anterior, posterior, dorsal, ventral, and lateral views; scale represents two millimeters.









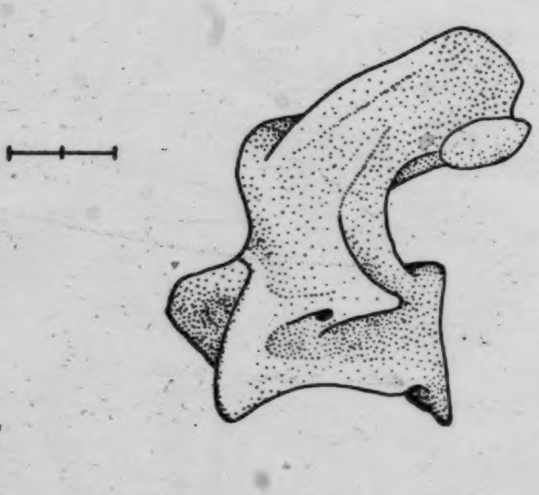


Figure 12. Midtrunk vertebrae in dorsal, ventral, and lateral views: (A) *Necturus maculosus*; (B) *Siren lacertina*; scale represents one millimeter.

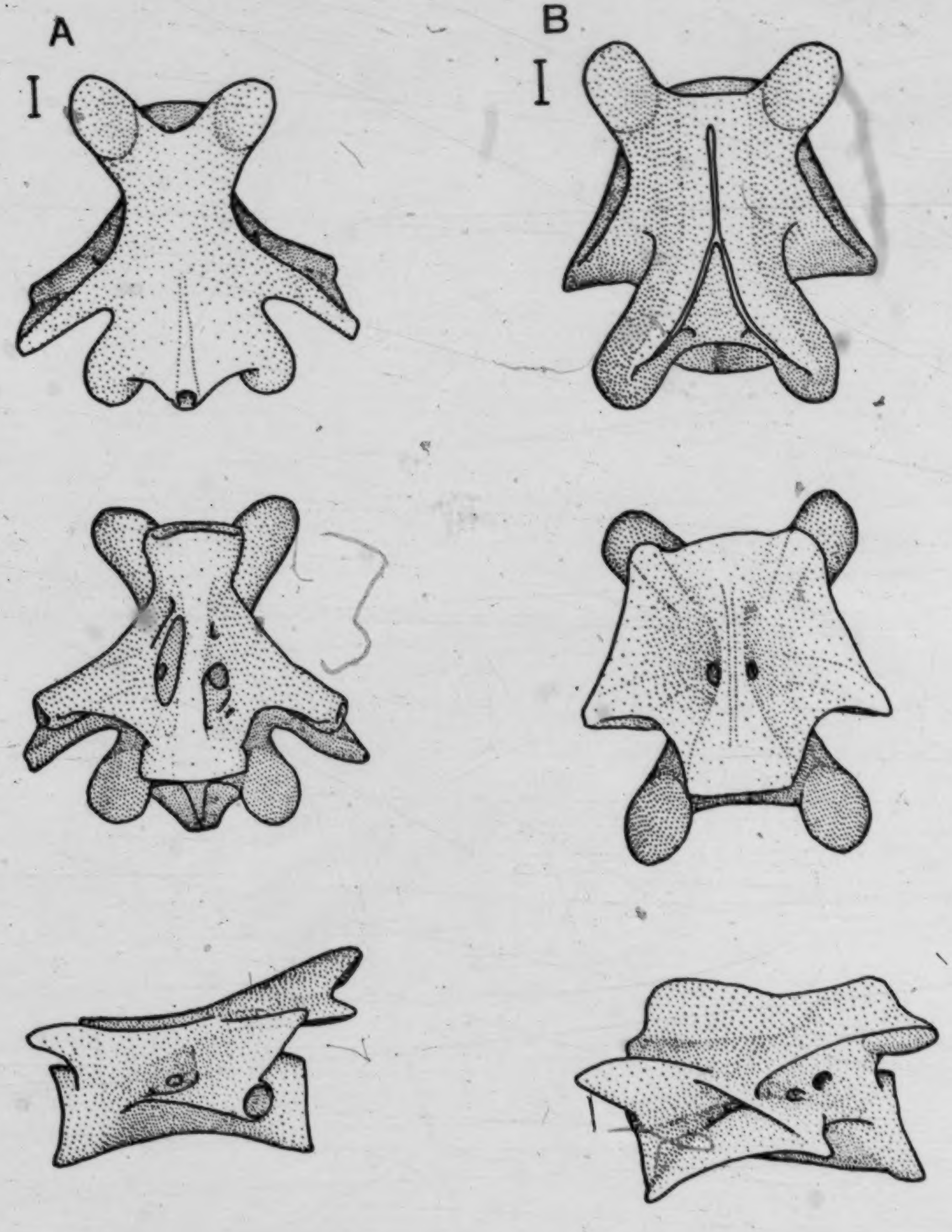

A
B

Figure 13. Trunk vertebrae of *Necturus* in dorsal, ventral, and lateral views: (A) UA 14310; (B) UA 14311; both from the Paleocene Ravenscrag Formation, Saskatchewan; scale represents one millimeter;

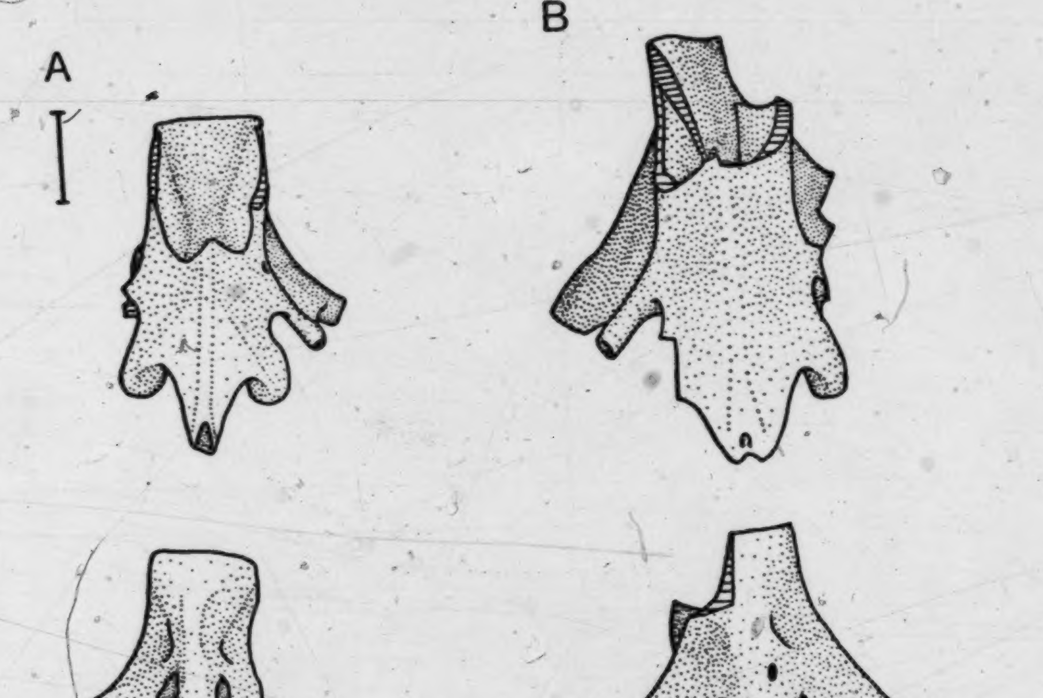

A
B

Figure 14. Midtrunk vertebrae of plethodontid salamanders in dorsal, ventral, and lateral views: (A) *Plethodon jordani*; (B) *Aneides lugubris*, T8; scale represents one millimeter.

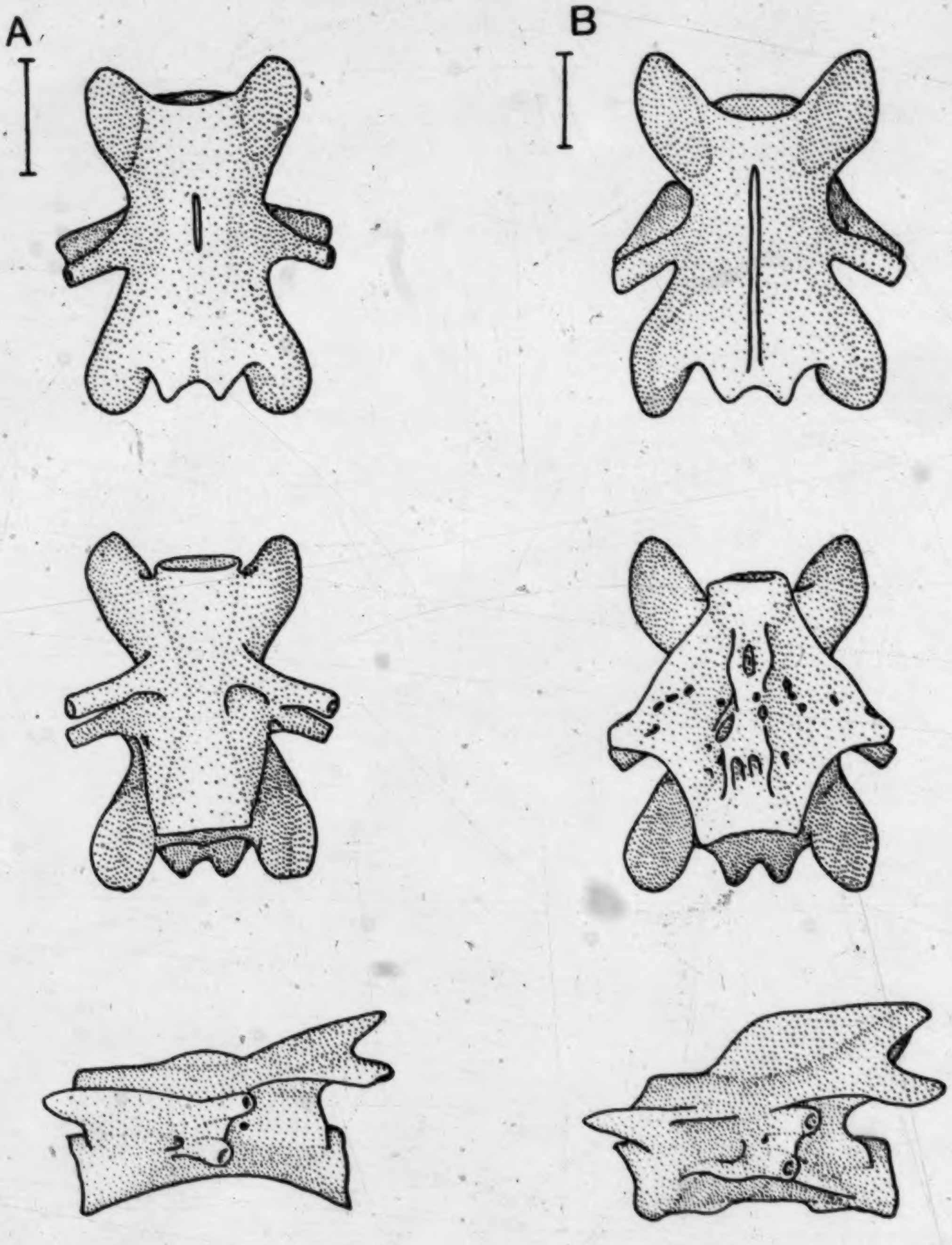
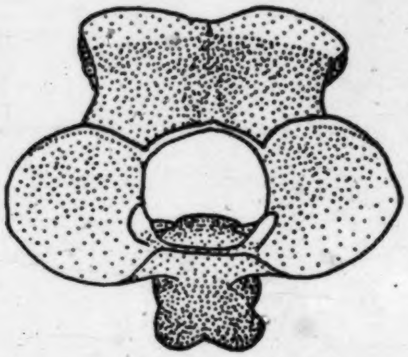
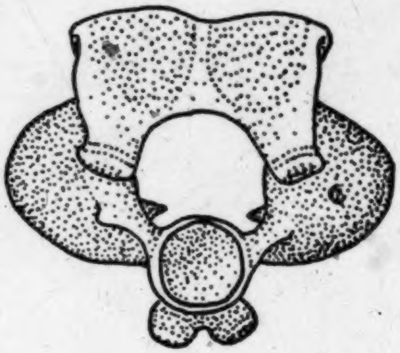
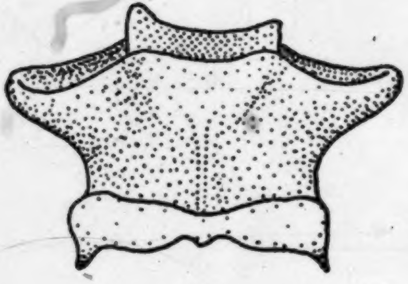
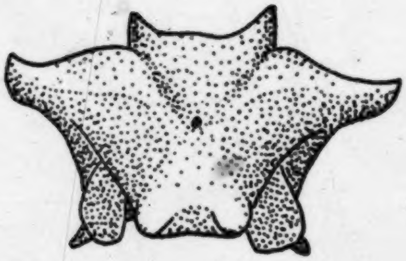

A
B

Figure 15. Atlas of *Desmognathus fuscus* in anterior, posterior, dorsal, ventral, and lateral views; scale represents two millimeters.









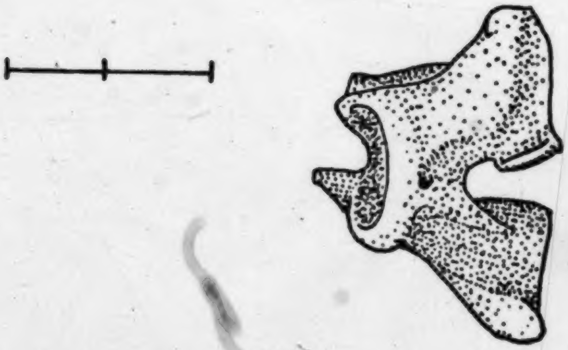


Figure 16. Midtrunk vertebrae of plethodontid salamanders in dorsal, ventral, and lateral views: (A) *Pseudotriton ruber*, T8: (B) *Desmognathus fuscus*; scale represents one millimeter.

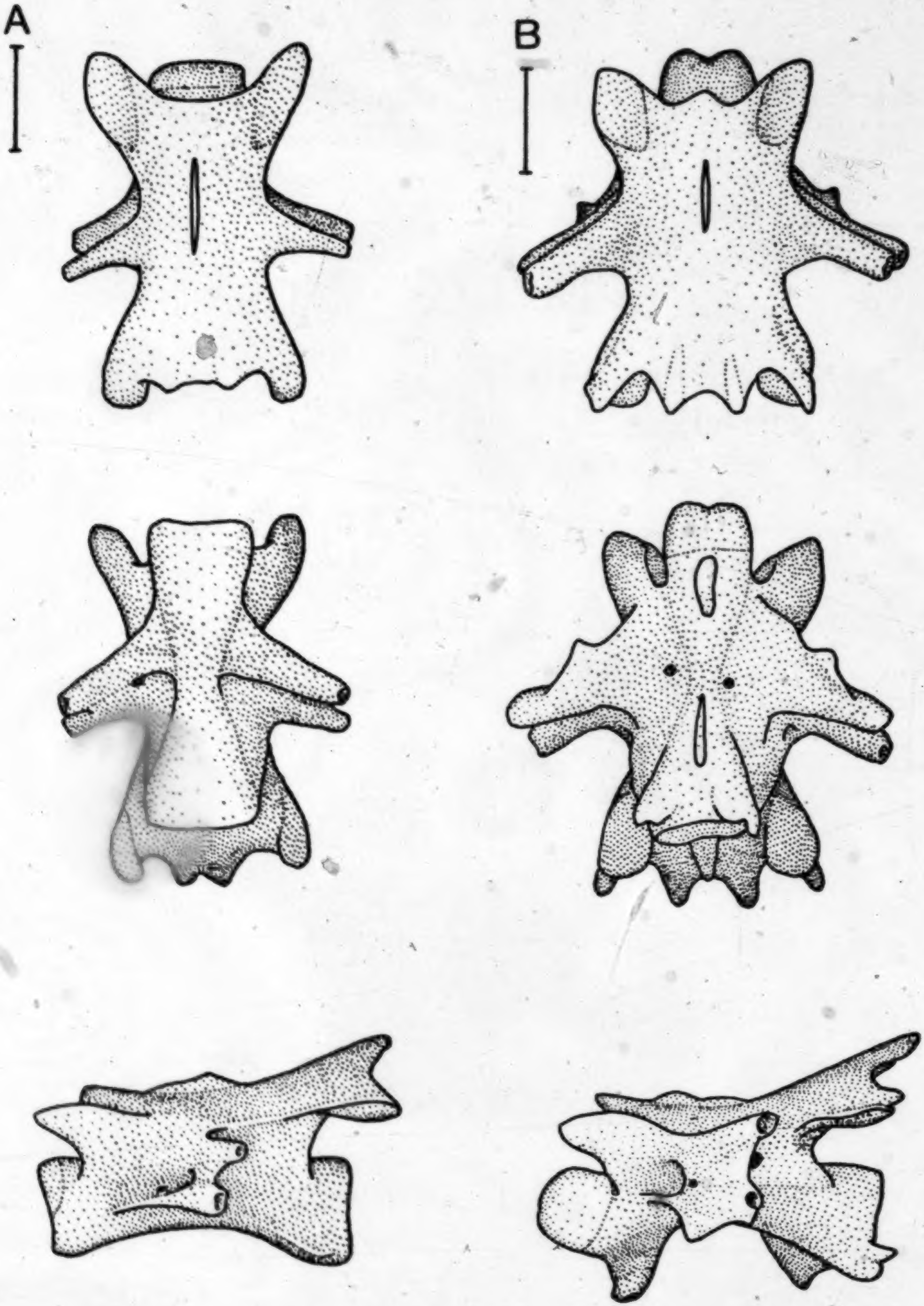
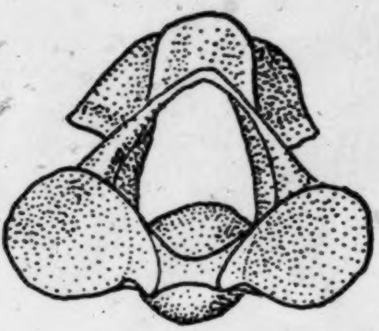
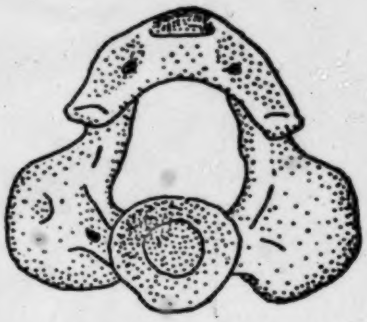
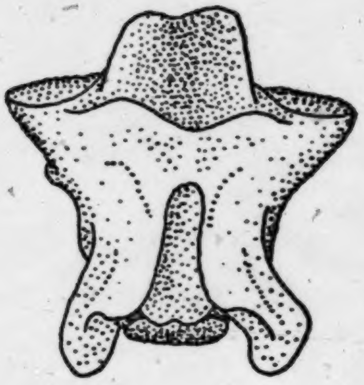
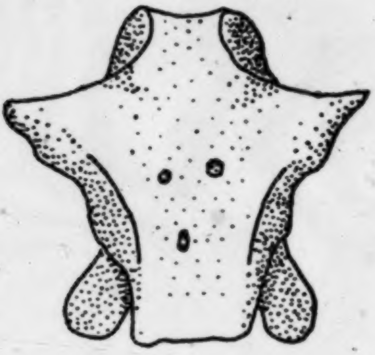

A
B

Figure 17. Atlas of *Salamandra salamandra* in anterior, posterior, dorsal, ventral, and lateral views; scale represents two millimeters.









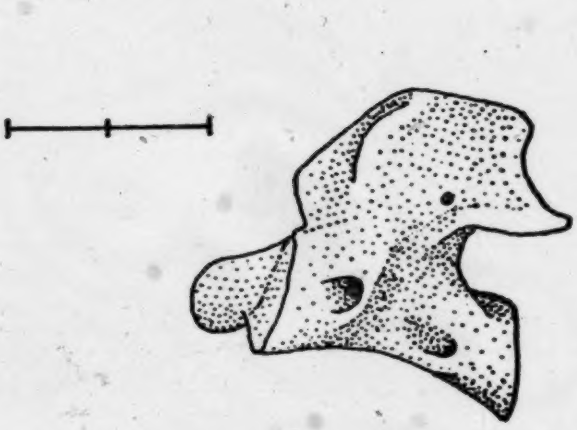


Figure 18. Midtrunk vertebrae of salamandrid salamanders in dorsal, ventral, and lateral views: (A) *Salamandra salamandra*; (B) *Pleurodeles waltli*, T8; scale represents one millimeter.

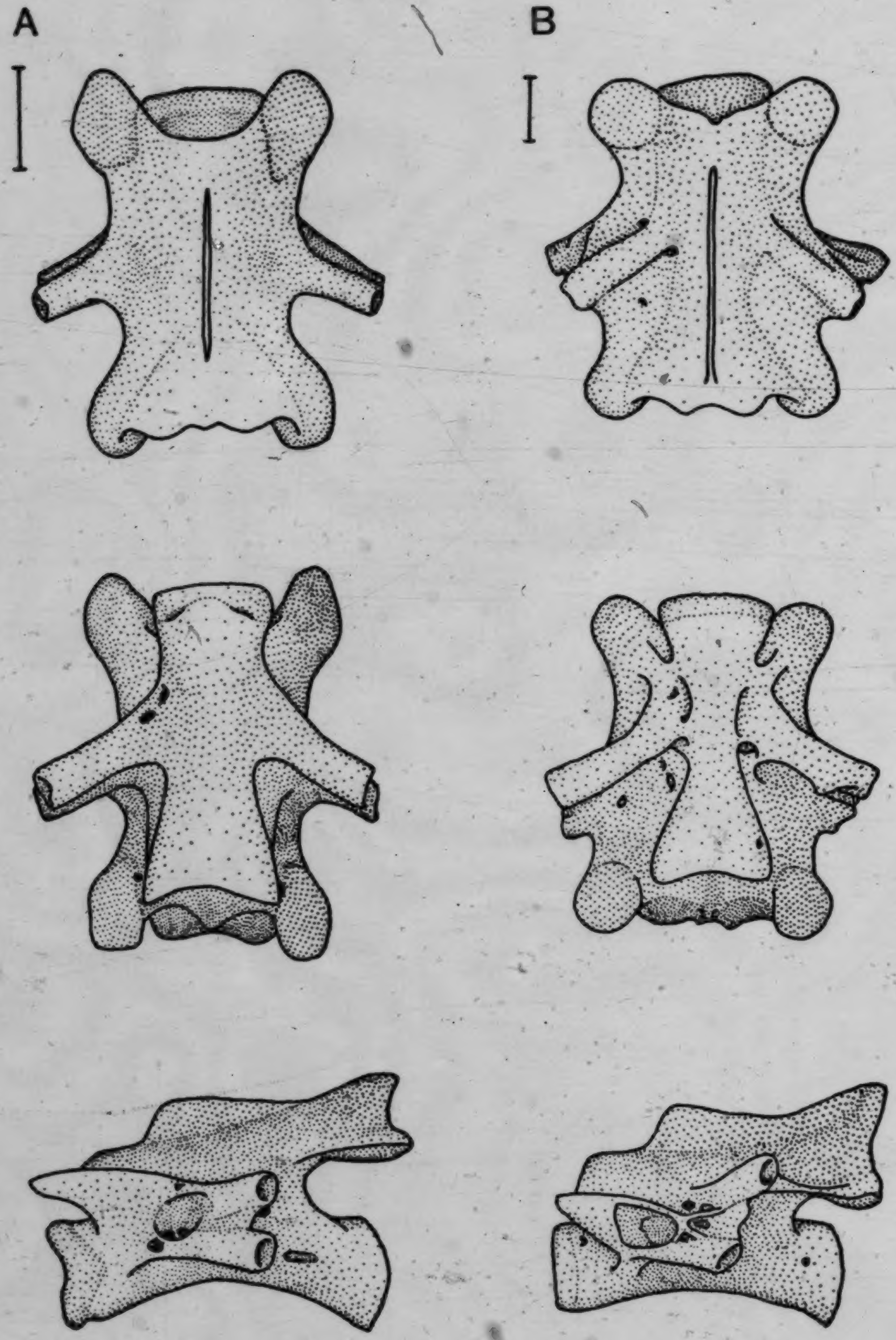
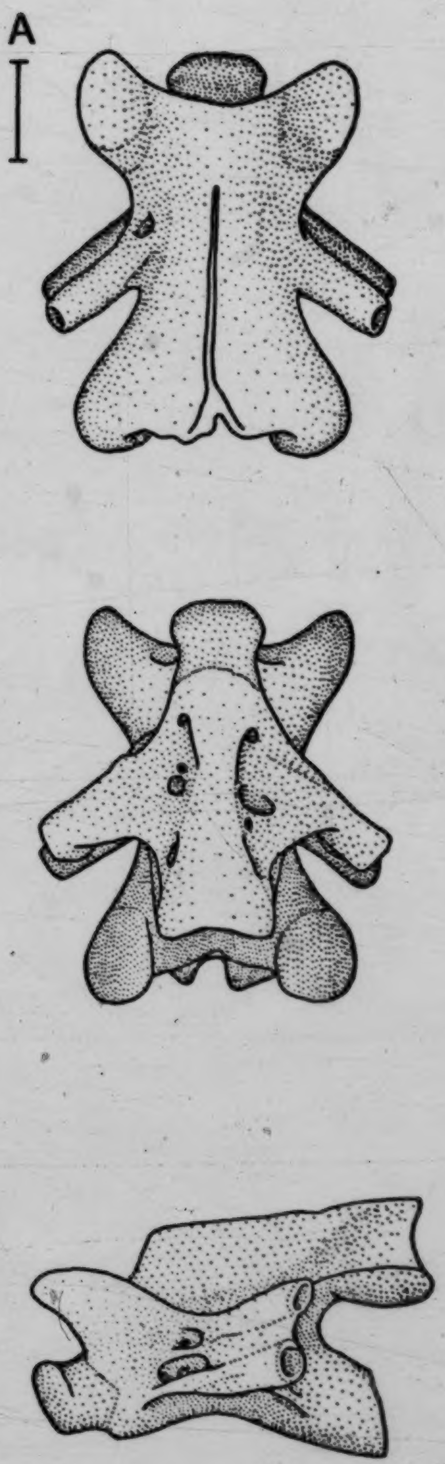

A
B

Figure 19. Midtrunk vertebrae of North American salamandrids in dorsal, ventral, and lateral views: (A) *Taricha* species, T7; (B) *Notophthalmus viridescens*, T7; scale represents one millimeter.


A

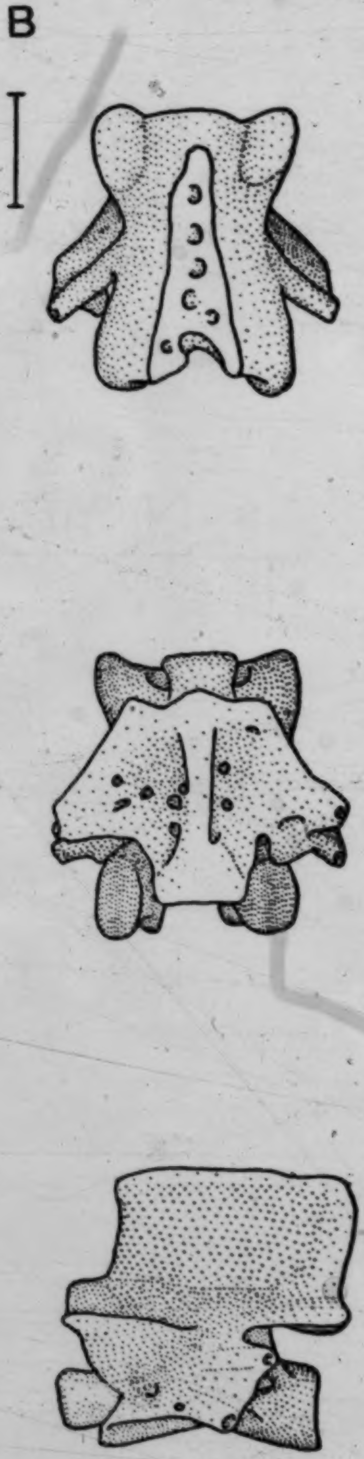
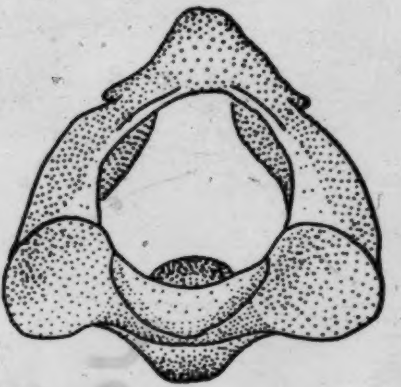
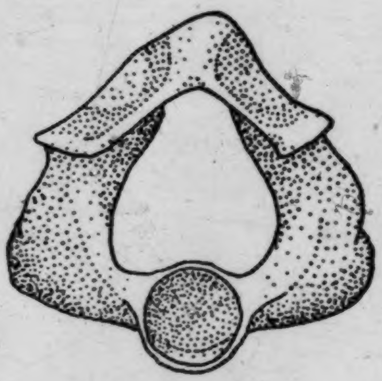
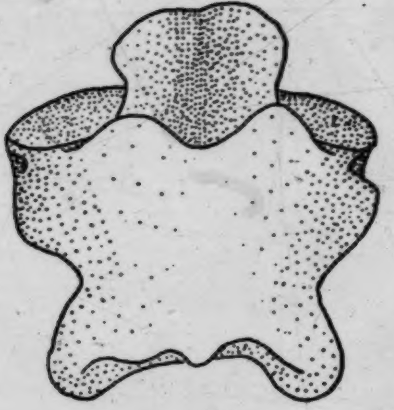
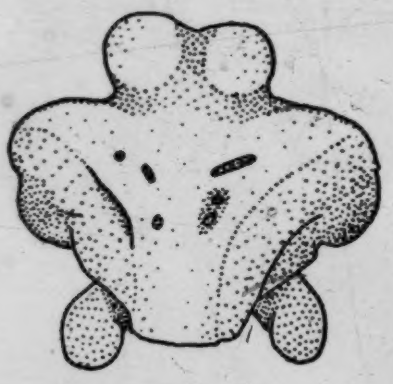

B

Figure 20. Atlas of *Triturus alpestris* in anterior, posterior, dorsal, ventral, and lateral views; scale represents one millimeter.









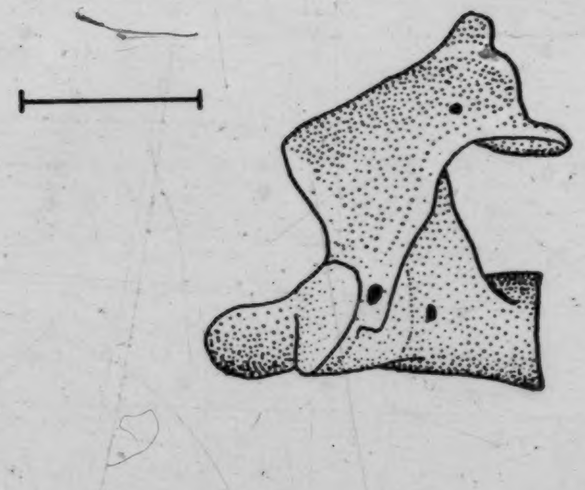


Figure 21. Midtrunk vertebrae of salamandrid salamanders in dorsal, ventral, and lateral views: (A) *Triturus cristatus*, T8; (B) *Triturus vulgaris*, T8; scale represents one millimeter.

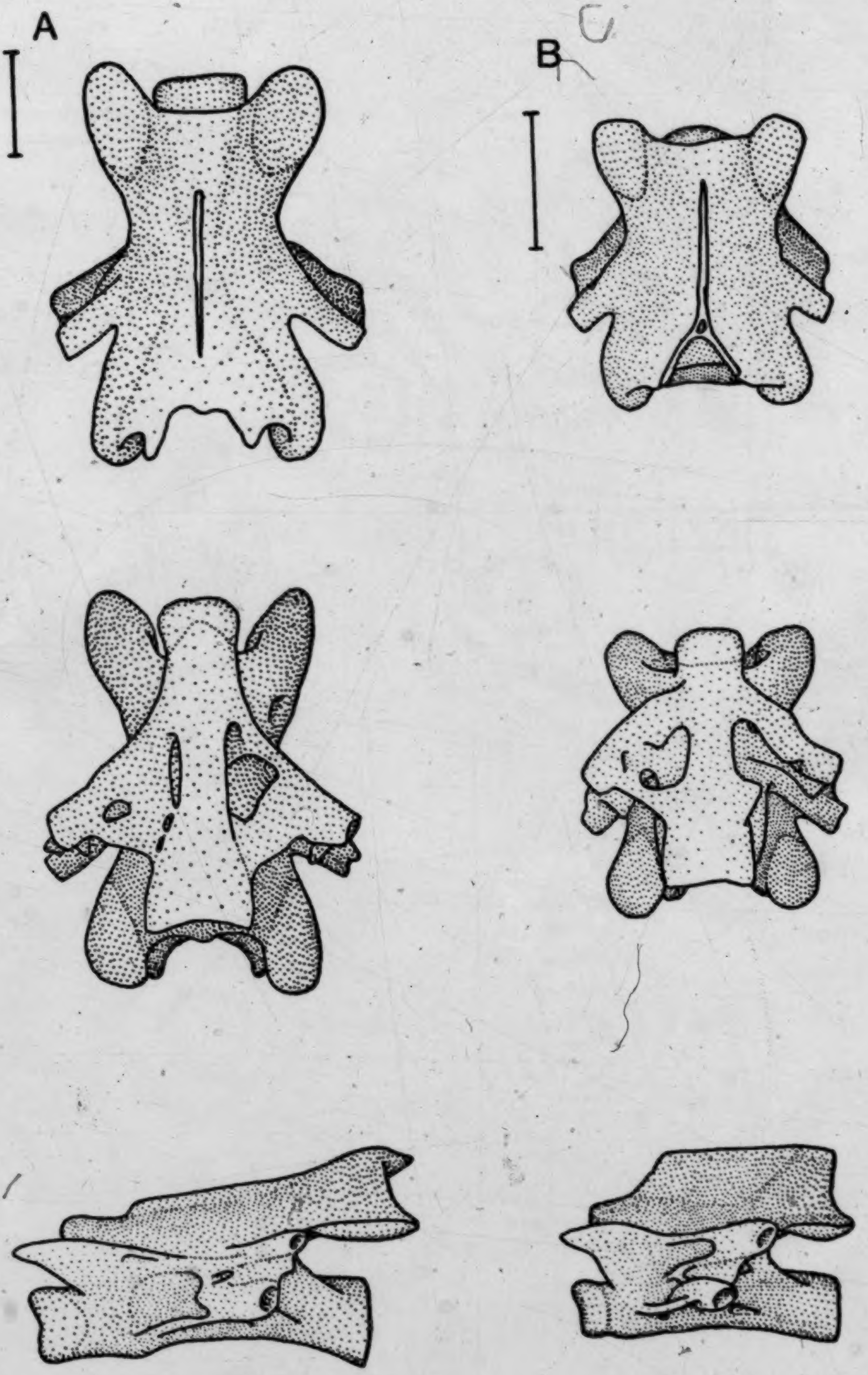

A
B

Figure 22. Dissection of *Hynobius retardatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

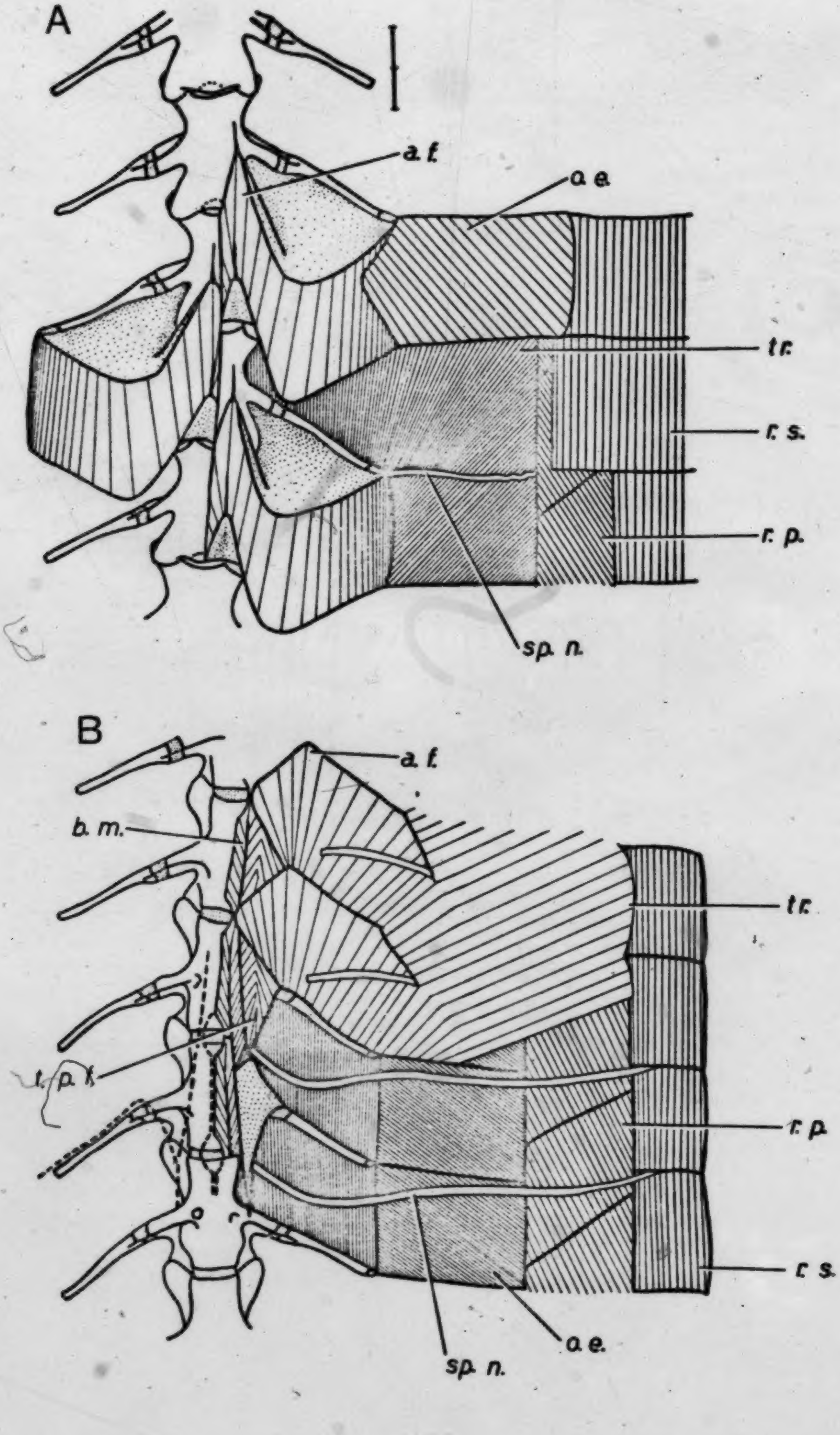

A
a. f.
a. e.
tr.
r. s.
r. p.
sp. n.
B
a. f.
b. m.
tr.
t. p. l.
r. p.
r. s.
a. e.
sp. n.

Figure 23. Dissection of *Hynobius naevius* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

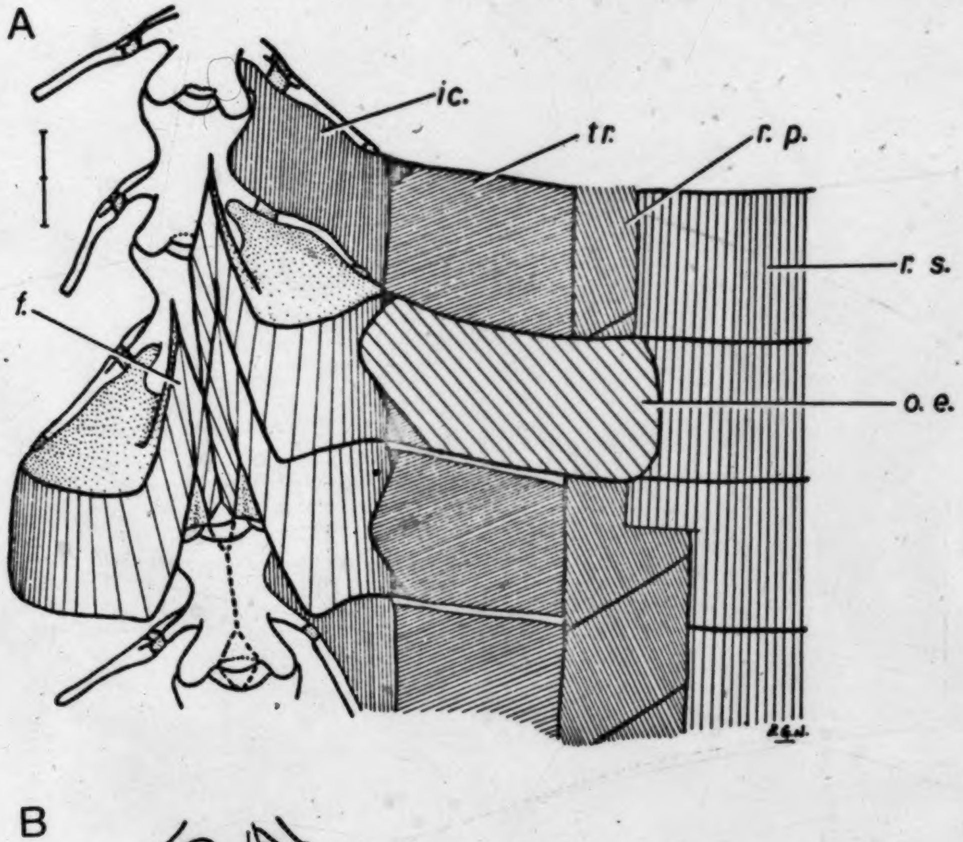

A
ic.
tr.
r. p.
r. s.
a. f.
o. e.
B
sp. n.
b. m.
tr.
r. s.
t. p. f.
r. p.
o. e.

Figure 24. Dissection of *Pachypalaminus boulengeri* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

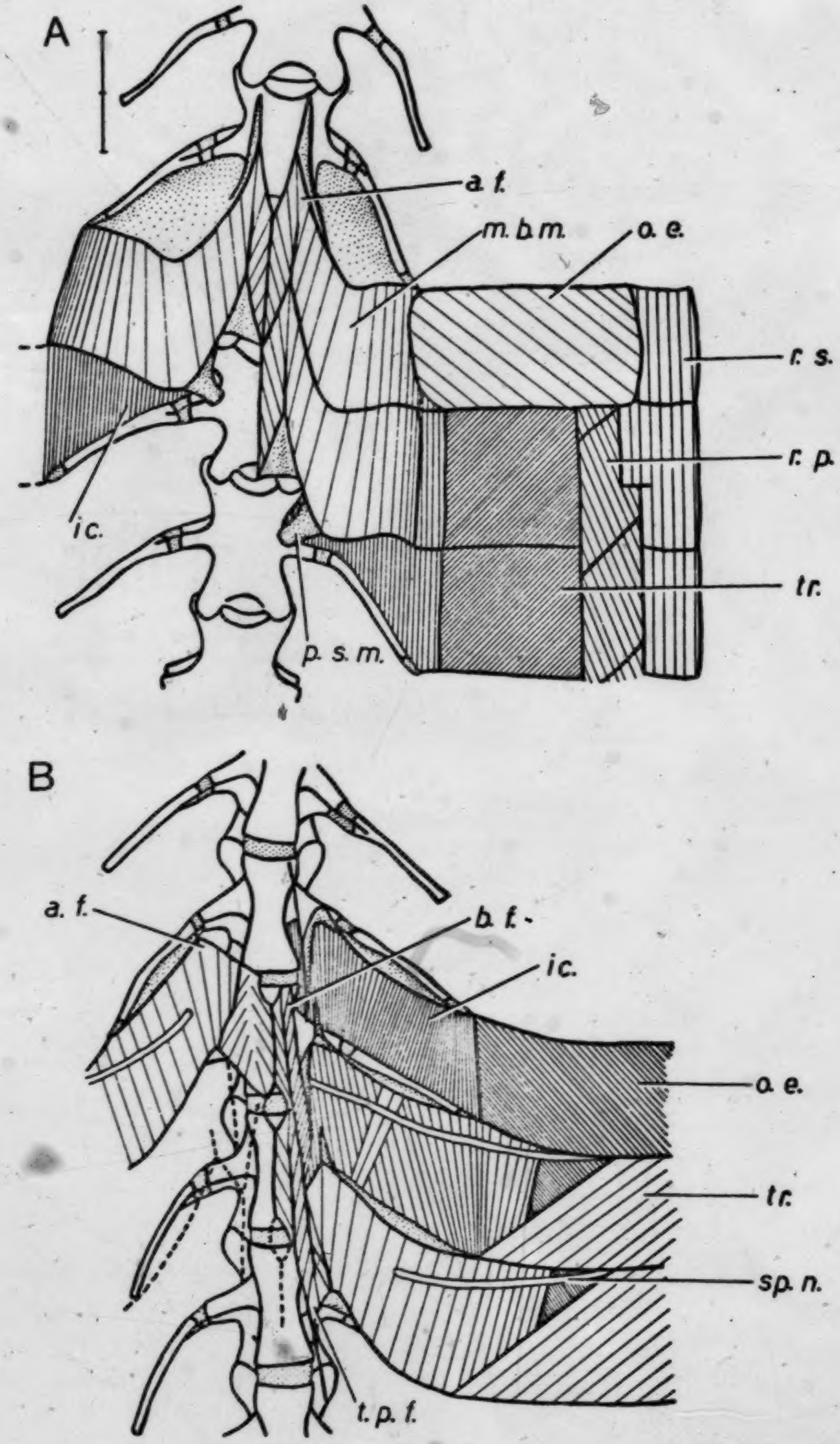

A
a. f.
m. b. m.
o. e.
r. s.
r. p.
tr.
i c.
p. s. m.
B
a. f.
b. f.
ic.
o. e.
tr.
sp. n.
t. p. f.

Figure 25. Dissection of *Onychodactylus japonicus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

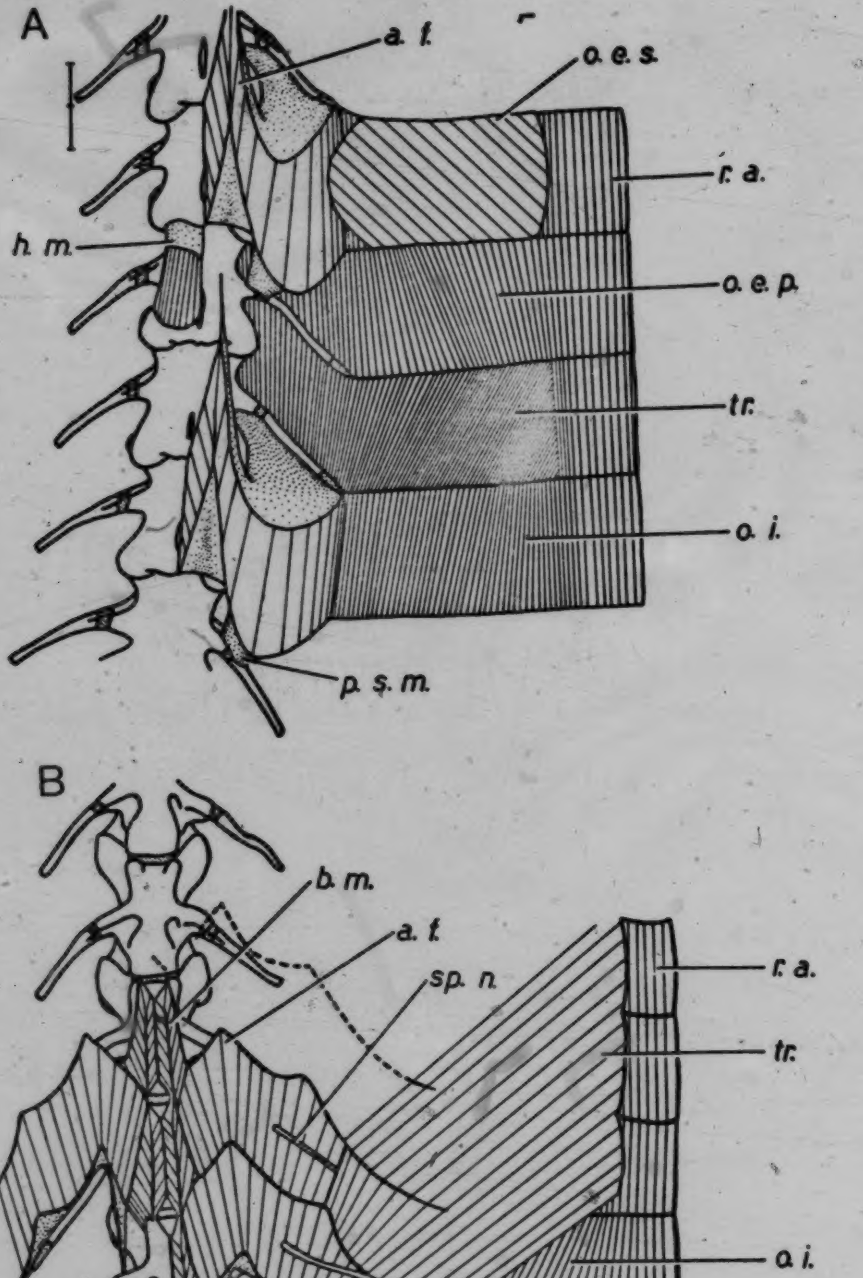

A
a. f.
o. e. s.
r. a.
h. m.
o. e. p.
tr.
o. i.
p. s. m.
B
b. m.
a. f.
sp. n.
r. a.
tr.
o. i.
o. e. p.

Figure 26. Cross-sections through the trunk musculature of hynobiid and ambystomatid salamanders: (A) *Hynobius*; (B) *Onychodactylus*; (C) *Ambystoma jeffersonianum*; (D) *Ambystoma talpoideum*; abbreviations given on pp. 4-7.

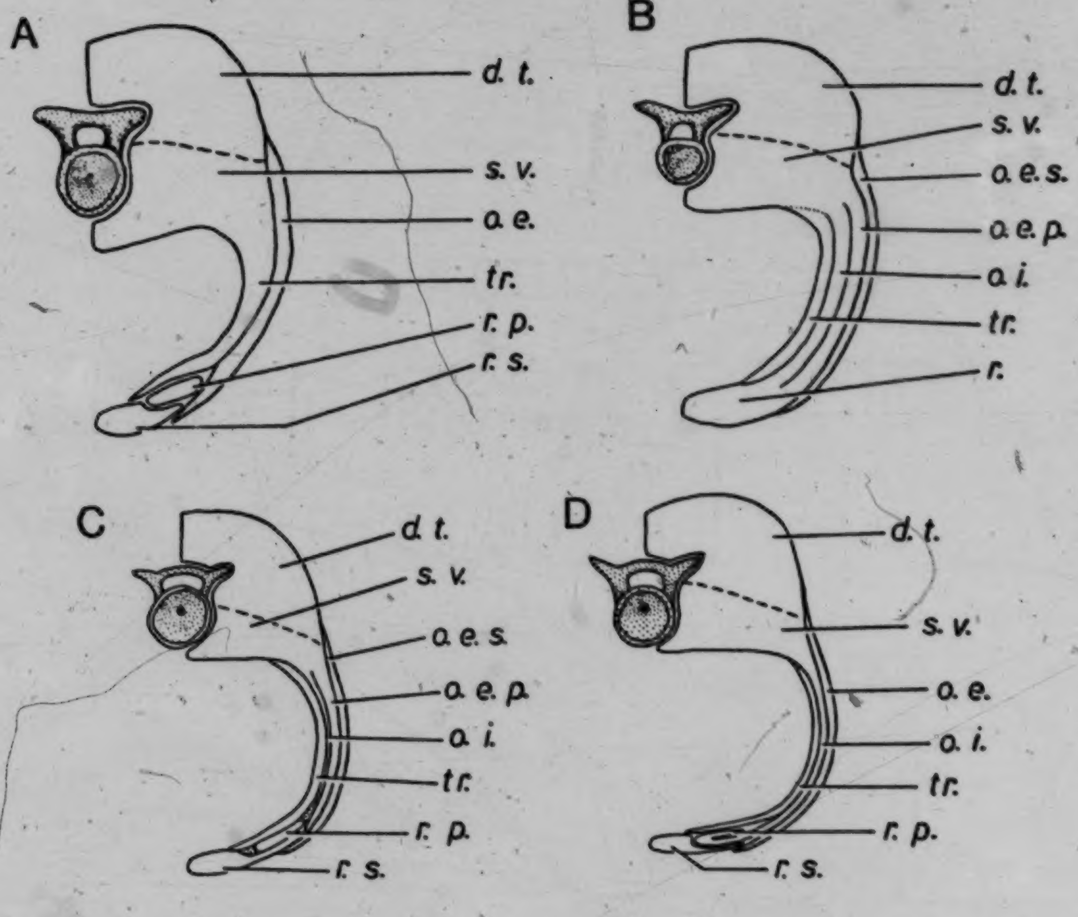

A
d. t.
s. v.
a. e.
tr.
r. p.
r. s.
B
d. t.
s. v.
a. e. s.
a. e. p.
a. i.
tr.
r.
C
d. t.
s. v.
a. e. s.
a. e. p.
a. i.
tr.
r. p.
r. s.
D
d. t.
s. v.
a. e.
a. i.
tr.
r. p.
r. s.

Figure 27. Dissection of *Cryptobranchus alleganiensis* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, lateral abdominal musculature not shown complete; scale represents two millimeters; abbreviations given on pp. 4-7.

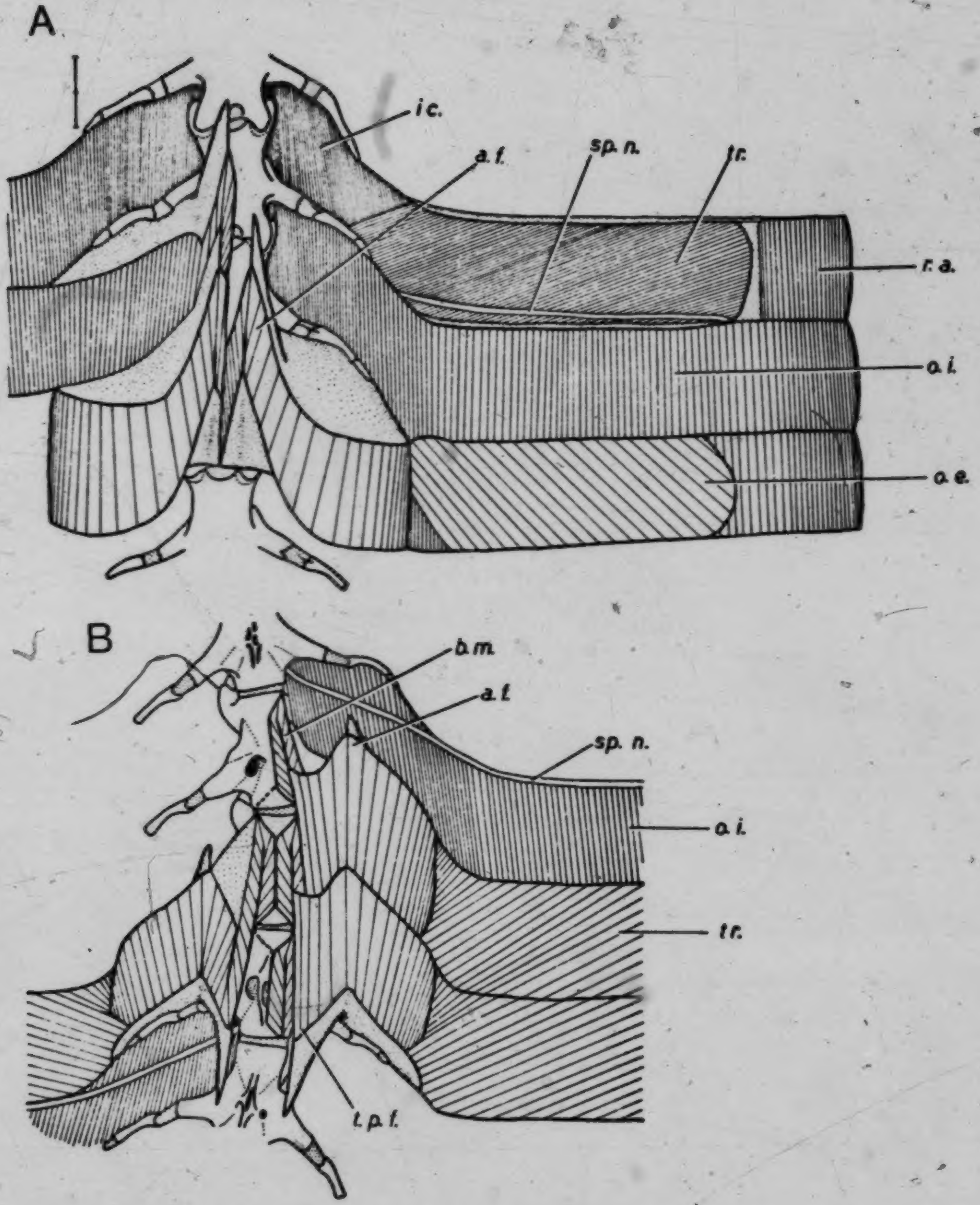

A
i.c.
a.f.
sp. n.
tr.
r. a.
a.i.
a.e.
B
b.m.
a.f.
sp. n.
a.i.
tr.
t.p.f.

Figure 28. Dissection of the axial musculature of *Amphiuma tridactylium* with the lateral abdominal musculature removed: (A) lateral view; (B) dorsal view; scale represents two millimeters; abbreviations given on pp. 4-7.

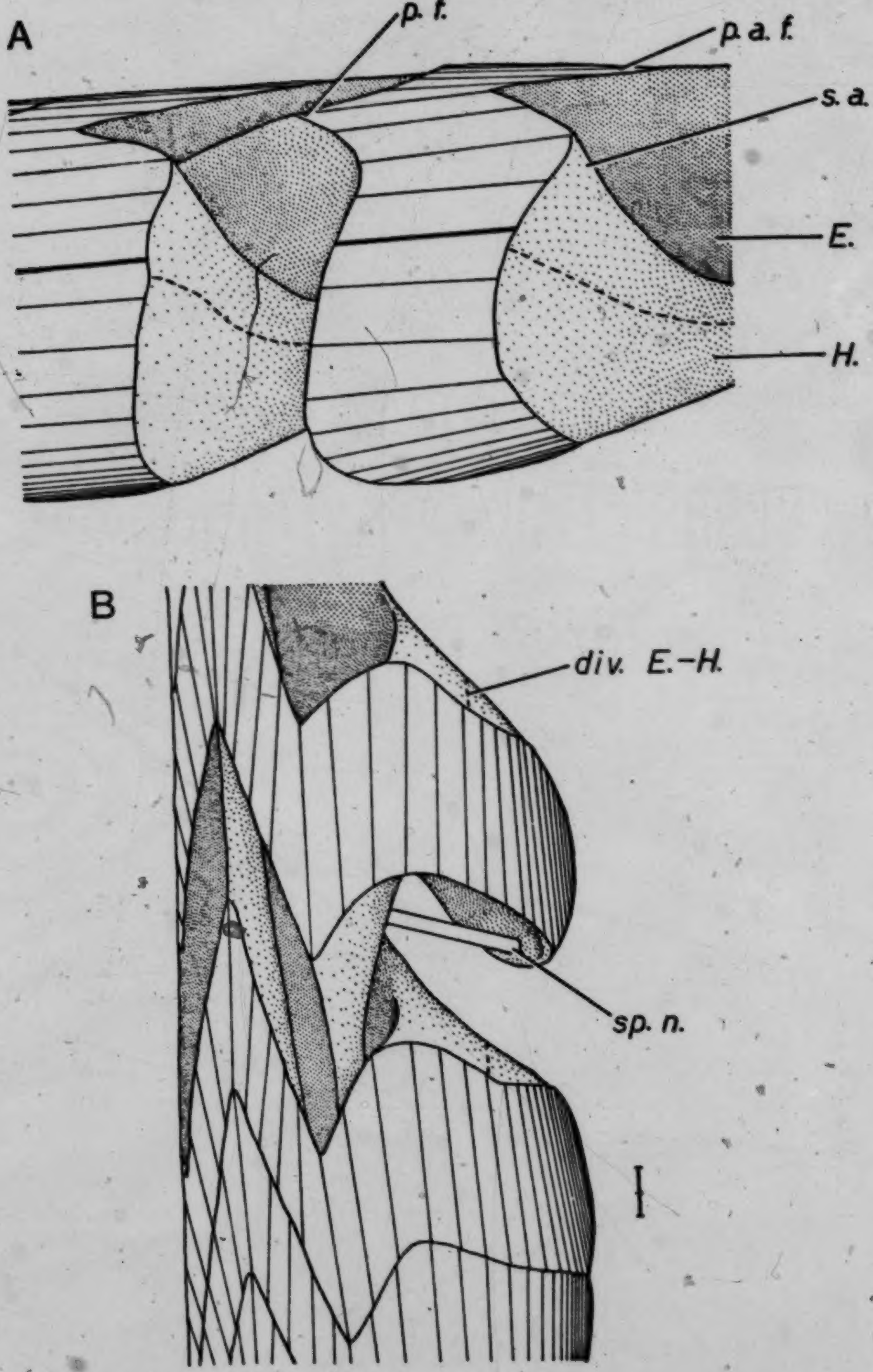
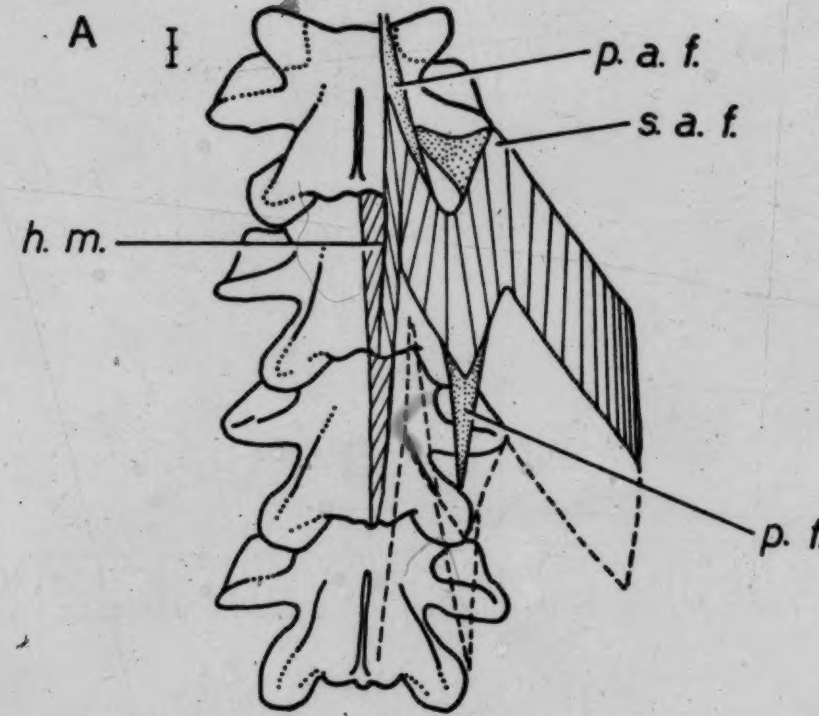

A
p. f.
p. a. f.
s. a. f.
E.
H.
B
div. E.-H.
sp. n.

Figure 29. Dissection of the epaxial musculature of *Amphiuma tridactylium* in dorsal views: (A) superficial unit; (B) deeper units, labelling following Auffenberg (1959); scale represents two millimeters; abbreviations given on pp. 4-7.


A
p. a. f.
s. a. f.
h. m.
p. f.

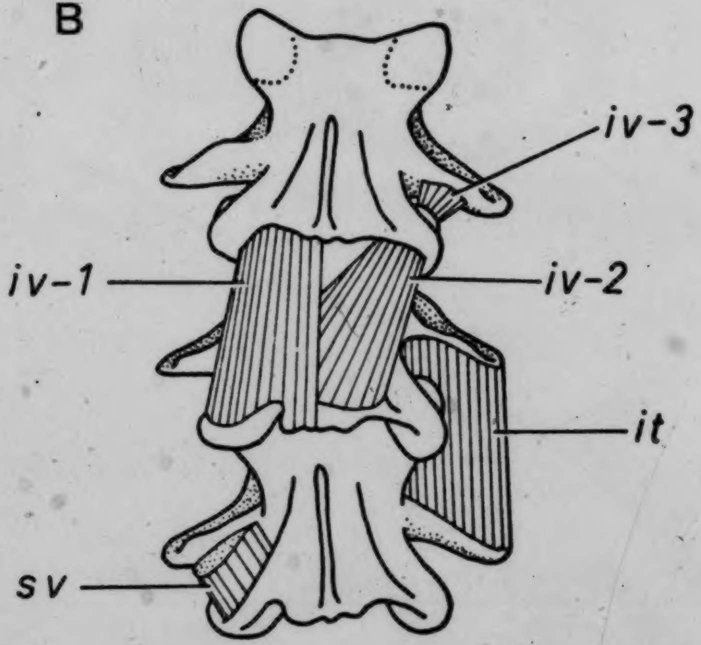

B
iv-3
iv-1
iv-2
it
sv

Figure 30. Dissection of the *subvertebralis* of *Amphiuma tridactylium* in ventral view; abbreviations given on pp. 4-7.

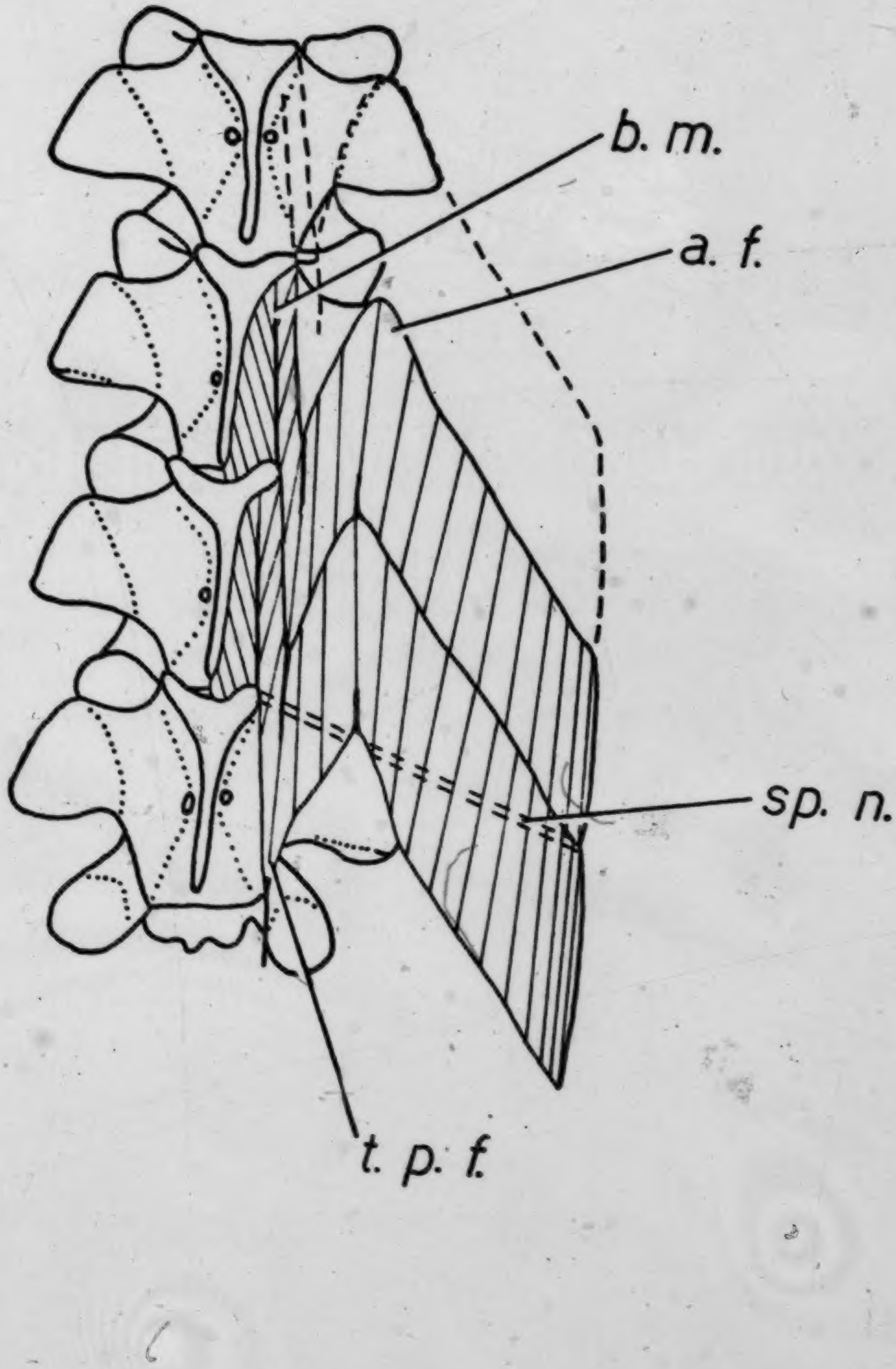

b. m.
a. f.
sp. n.
t. p. f.

Figure 31. Lateral abdominal musculature of *Amphiuma tridactylium* in lateral view; scale represents two millimeters; abbreviations given on pp. 4-7.

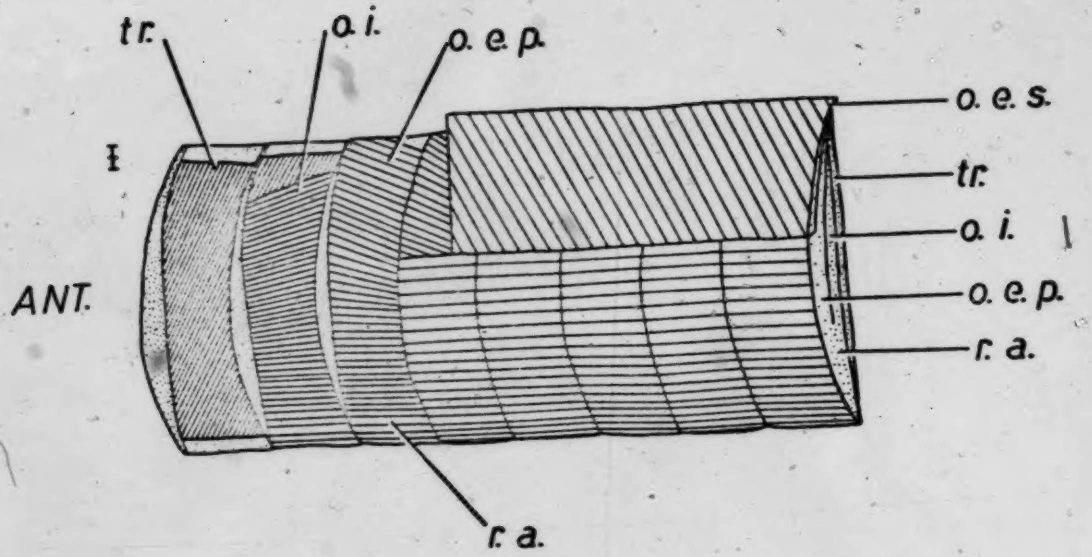

tr.
o. i.
o. e. p.
o. e. s.
tr.
o. i.
o. e. p.
r. a.
I
ANT.
r. a.

Figure 32. Cross-section through the trunk musculature of *Amphiuma tridactylium*; scale represents two millimeters; abbreviations given on pp. 4-7.

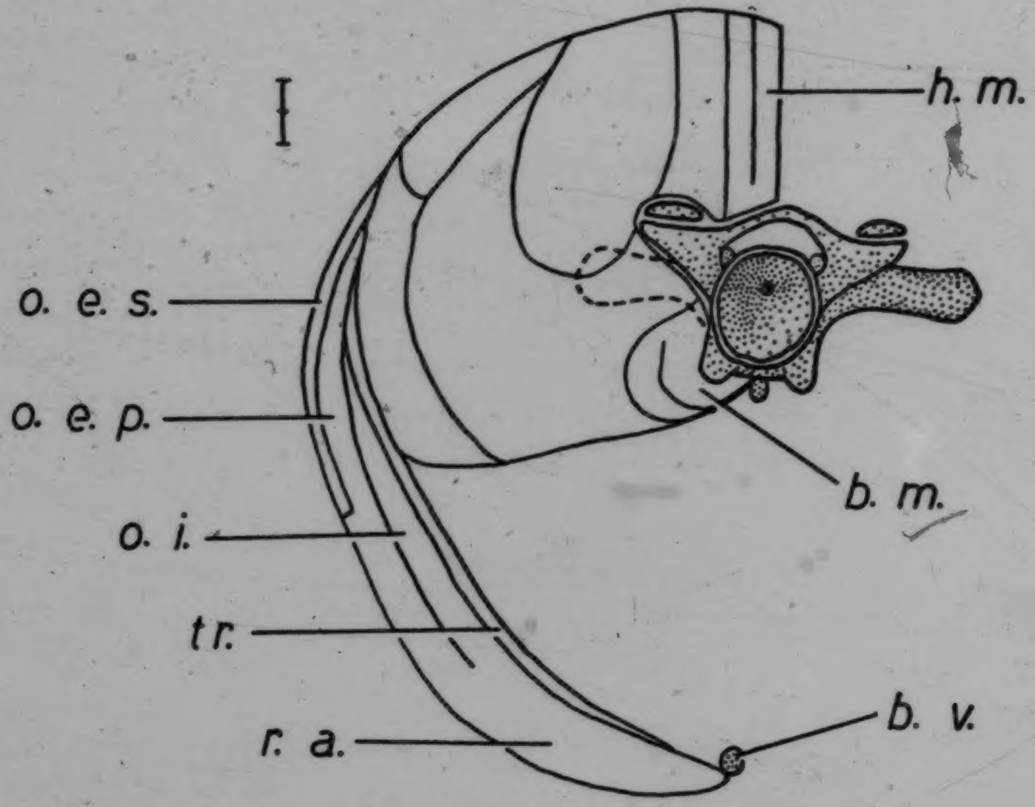

h. m.
o. e. s.
o. e. p.
b. m.
o. i.
tr.
b. v.
r. a.

Figure 33. Dissection of larval *Dicamptodon ensatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

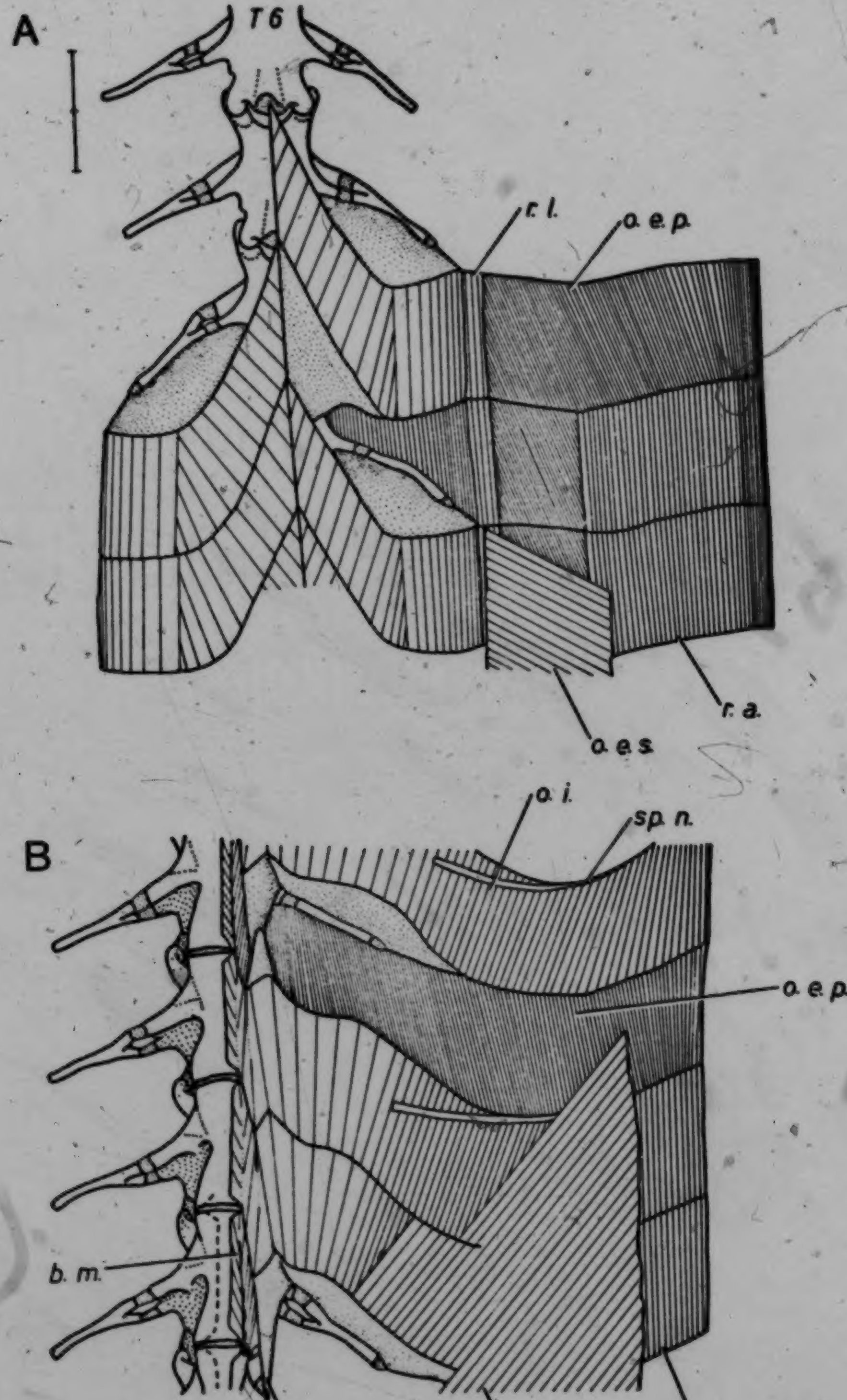

A
T6
r. l.
o. e. p.
r. a.
o. e. s.
B
o. i.
sp. n.
o. e. p.
b. m.
t. p. f.
tr.
r. a.

Figure 34. Dissection of metamorphosed adult *Dicamptodon ensatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

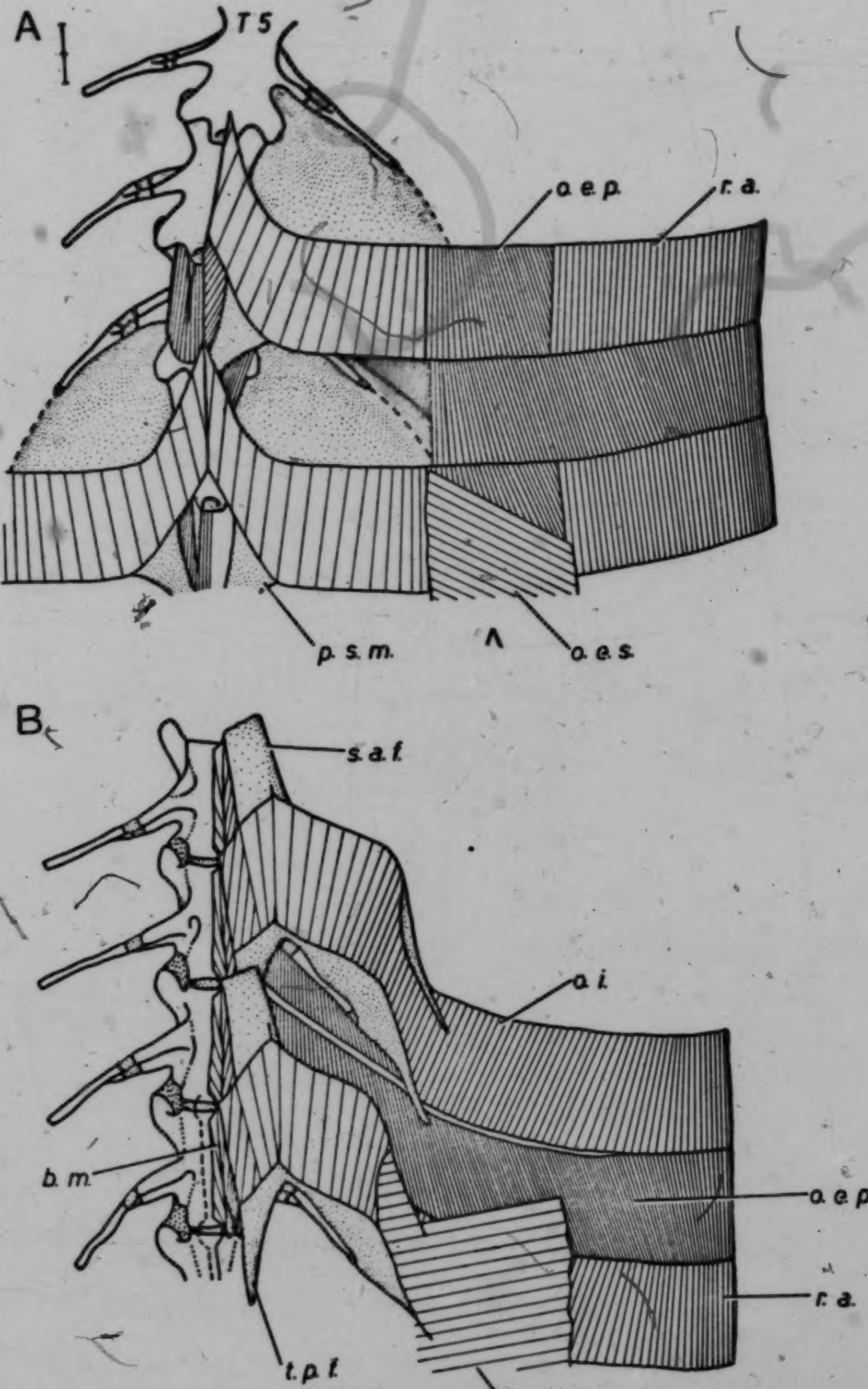

A
T5
o. e. p.
r. a.
p. s. m.
o. e. s.
B
s. a. f.
o. i.
b. m.
o. e. p.
r. a.
t. p. f.
tr.

Figure 35. Dissection of *Rhyacotriton olympicus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

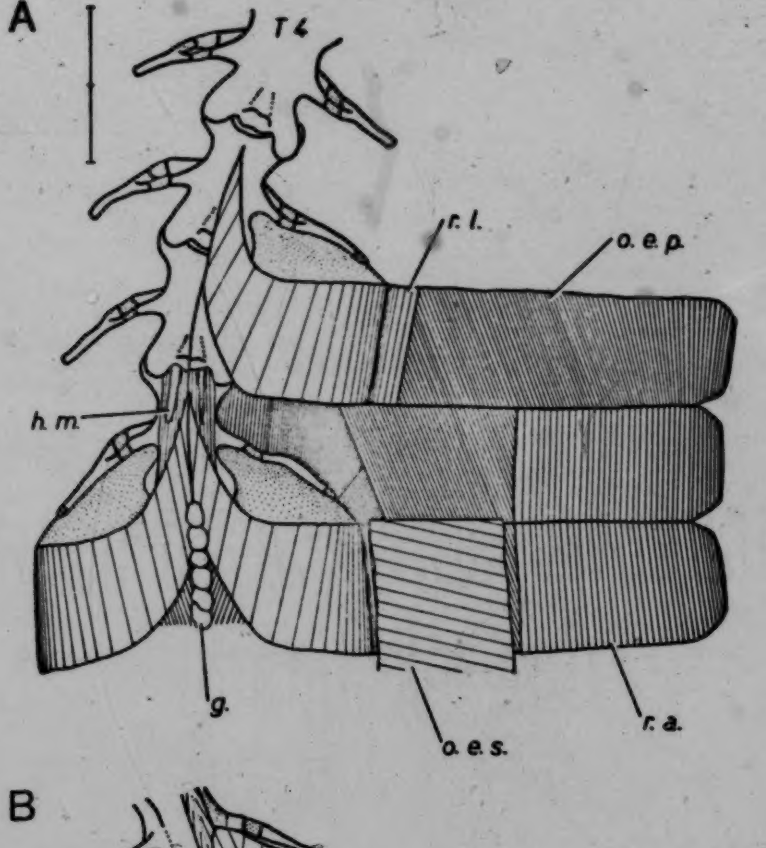

A
T4
r. l.
o. e. p.
h. m.
g.
o. e. s.
r. a.
B
o. i.
sp. n.
o. e. p.
p. b. m.
tr.

Figure 36. Dissection of *Ambystoma macrodactylum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

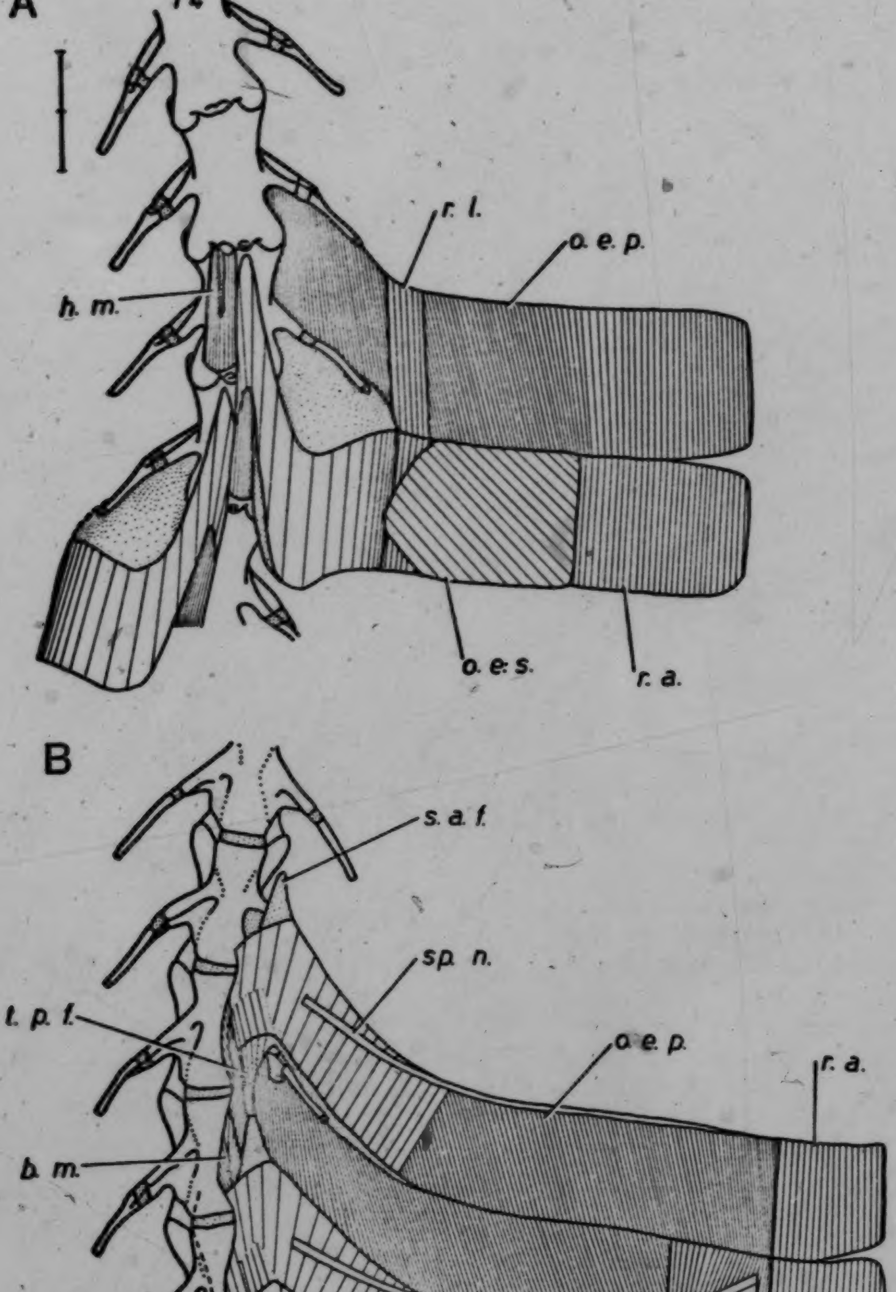

A
T4
r. l.
o. e. p.
h. m.
o. e. s.
r. a.
B
s. a. f.
sp. n.
t. p. f.
o. e. p.
r. a.
b. m.
tr.

Figure 37. Partial dissection of the trunk musculature of a larval *Ambystoma gracile* in lateral view; scale represents two millimeters; abbreviations given on pp. 4-7.

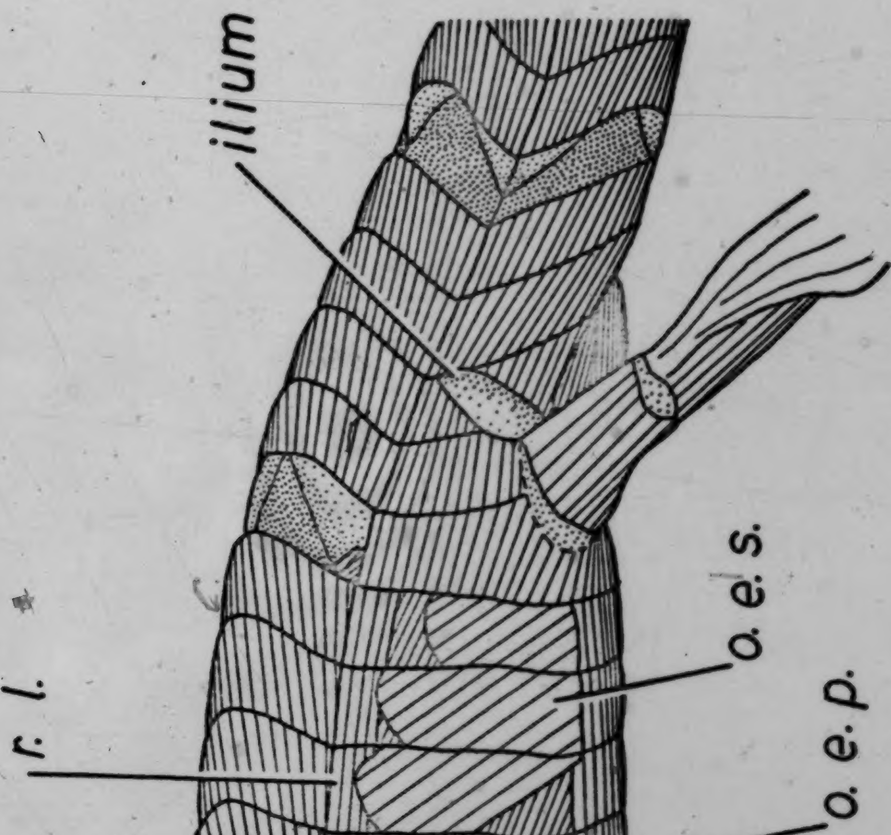
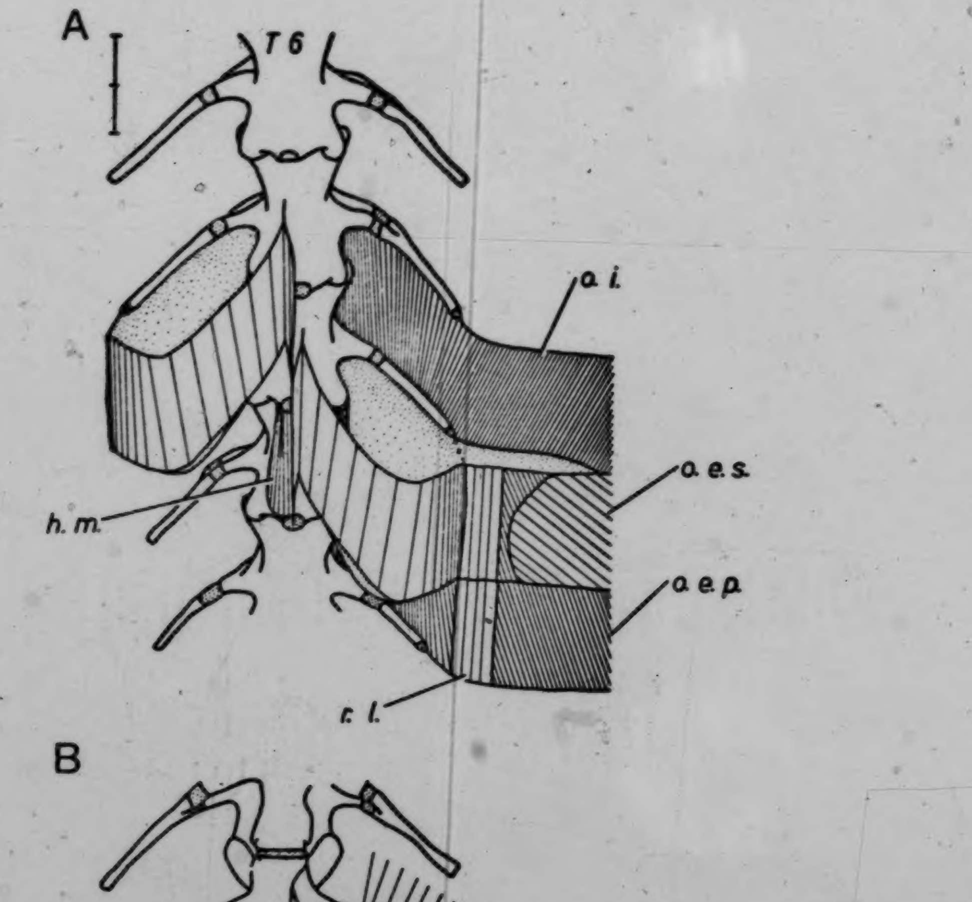

ilium
o. e. s.
o. e. p.
r. l.
a. f.
o. i.
r. a.

Figure 38. Dissection of larval *Ambystoma gracile* with lateral abdominal musculature spread laterally: (A) dorsal view; lateral abdominal musculature not shown complete; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.


A
T 6
a. i.
a. e. s.
h. m.
a. e. p.
r. l.
B
a. i.
t. p. f.
b. m.
a. e. p.
r. a.
sp. n.
tr.

a

Figure 39. Dissection of *Ambystoma maculatum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

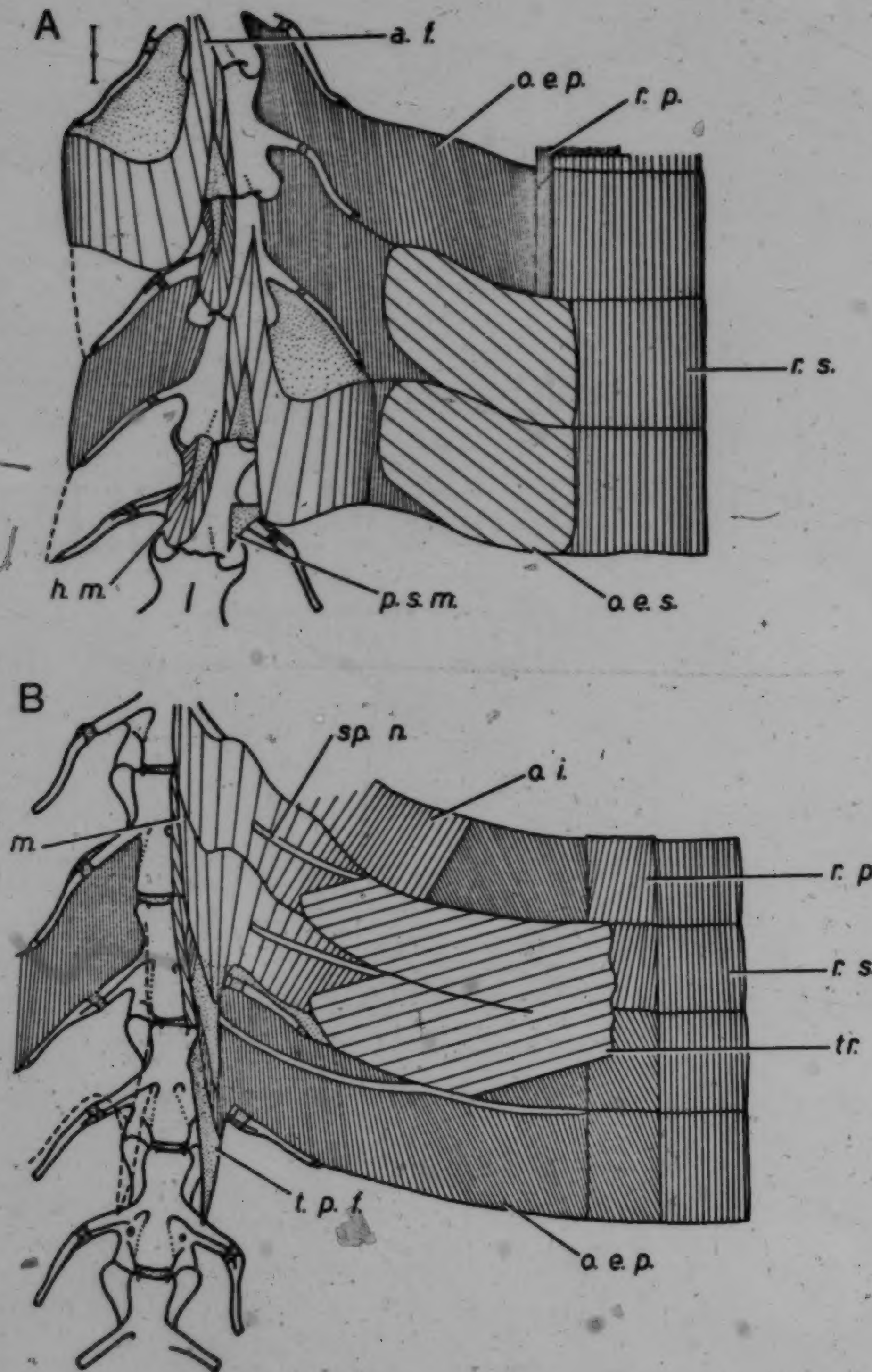

A
a. f.
o. e. p.
r. p.
r. s.
h. m.
p. s. m.
o. e. s.
B
sp. n.
o. i.
b. m.
r. p.
r. s.
tr.
t. p. f.
o. e. p.

Figure 40. Dissection of *Ambystoma jeffersonianum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents one millimeter; abbreviations given on pp. 4-7.

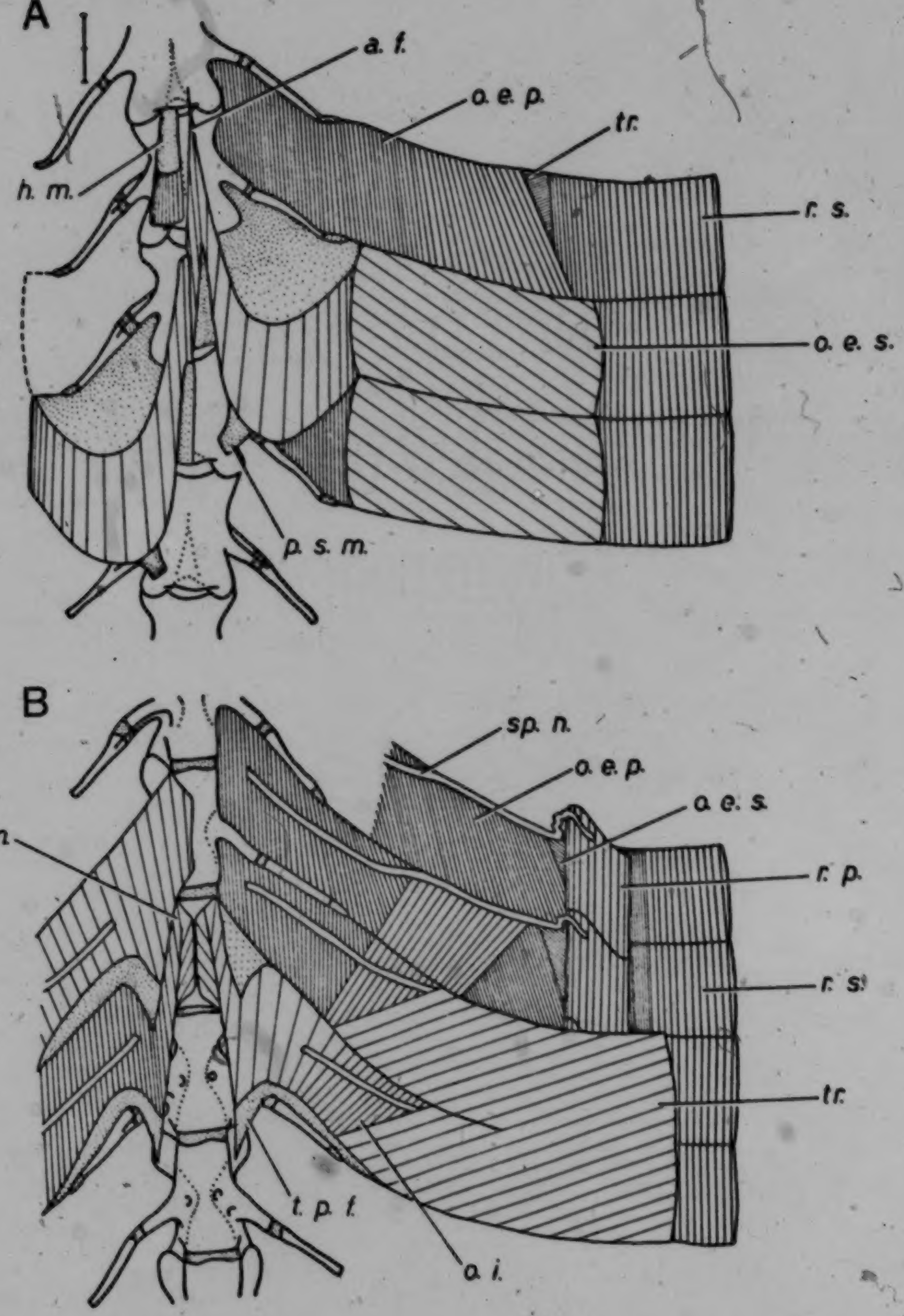

A
a. f.
o. e. p.
tr.
h. m.
r. s.
o. e. s.
p. s. m.
B
sp. n.
o. e. p.
b. m.
o. e. s.
r. p.
r. s.
tr.
t. p. f.
o. i.

Figure 41. Dissection of *Ambystoma opacum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

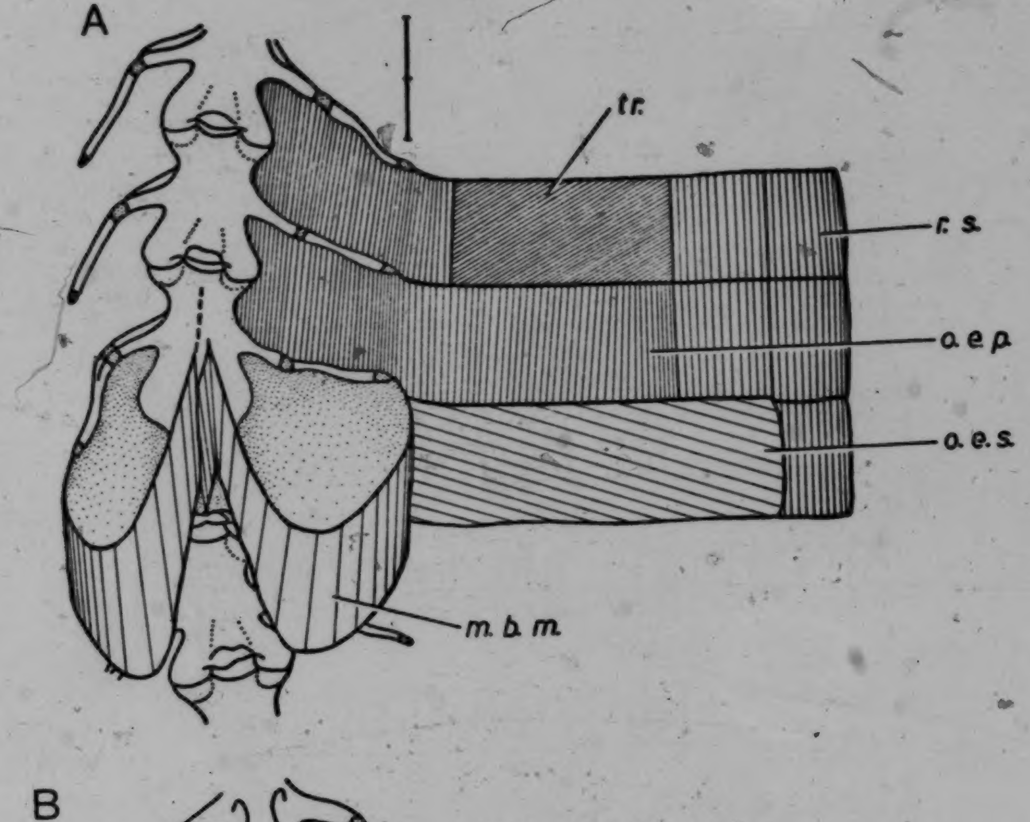
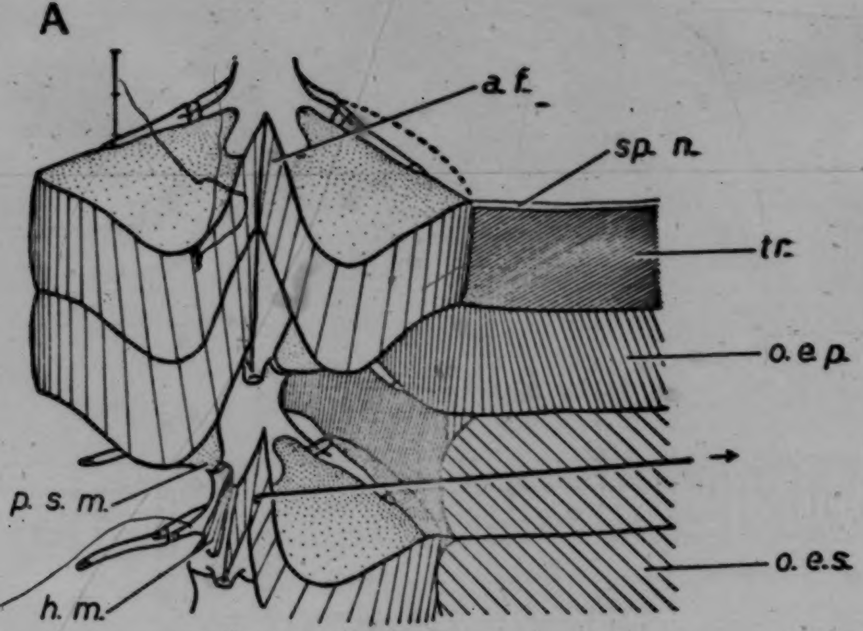

A
tr.
r. s.
a. e. p.
a. e. s.
m. b. m.
B
sp. n.
a. e. p.
r. p.
b. m.
r. s.
t. p. f.
tr.

Figure 42. Dissection of *Ambystoma talpoideum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.


A
a. f.
sp. n.
tr.
o. e. p.
p. s. m.
o. e. s.
h. m.

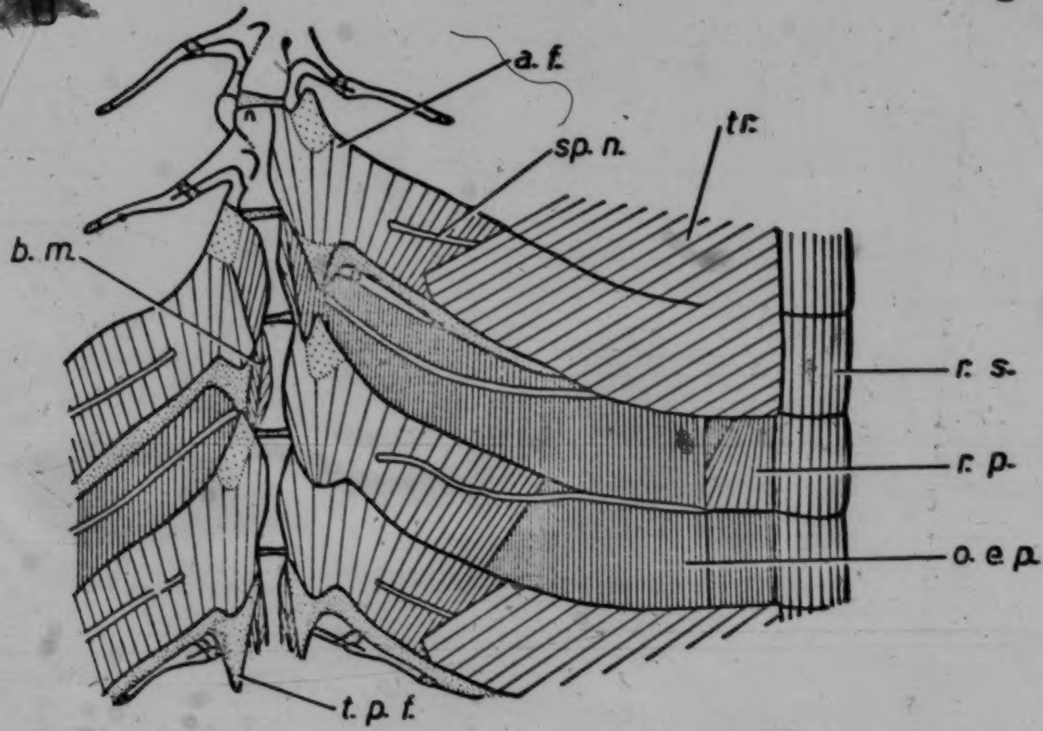

a. f.
tr.
sp. n.
b. m.
r. s.
r. p.
o. e. p.
t. p. f.

Figure 43. Dissection of larval *Ambystoma tigrinum* with lateral abdominal musculature not shown complete: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

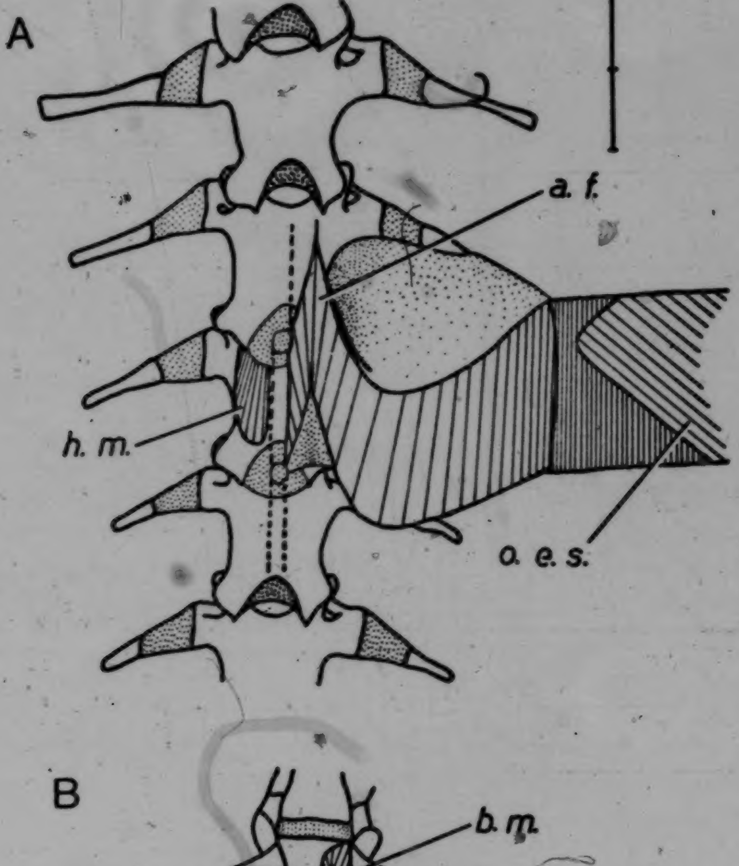

A
a. f.
h. m.
o. e. s.
B
b. m.
t. p. f.

Figure 44. Dissection of young metamorphosed *Ambystoma tigrinum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, lateral abdominal musculature not shown complete; scale represents two millimeters; abbreviations given on pp. 4-7.

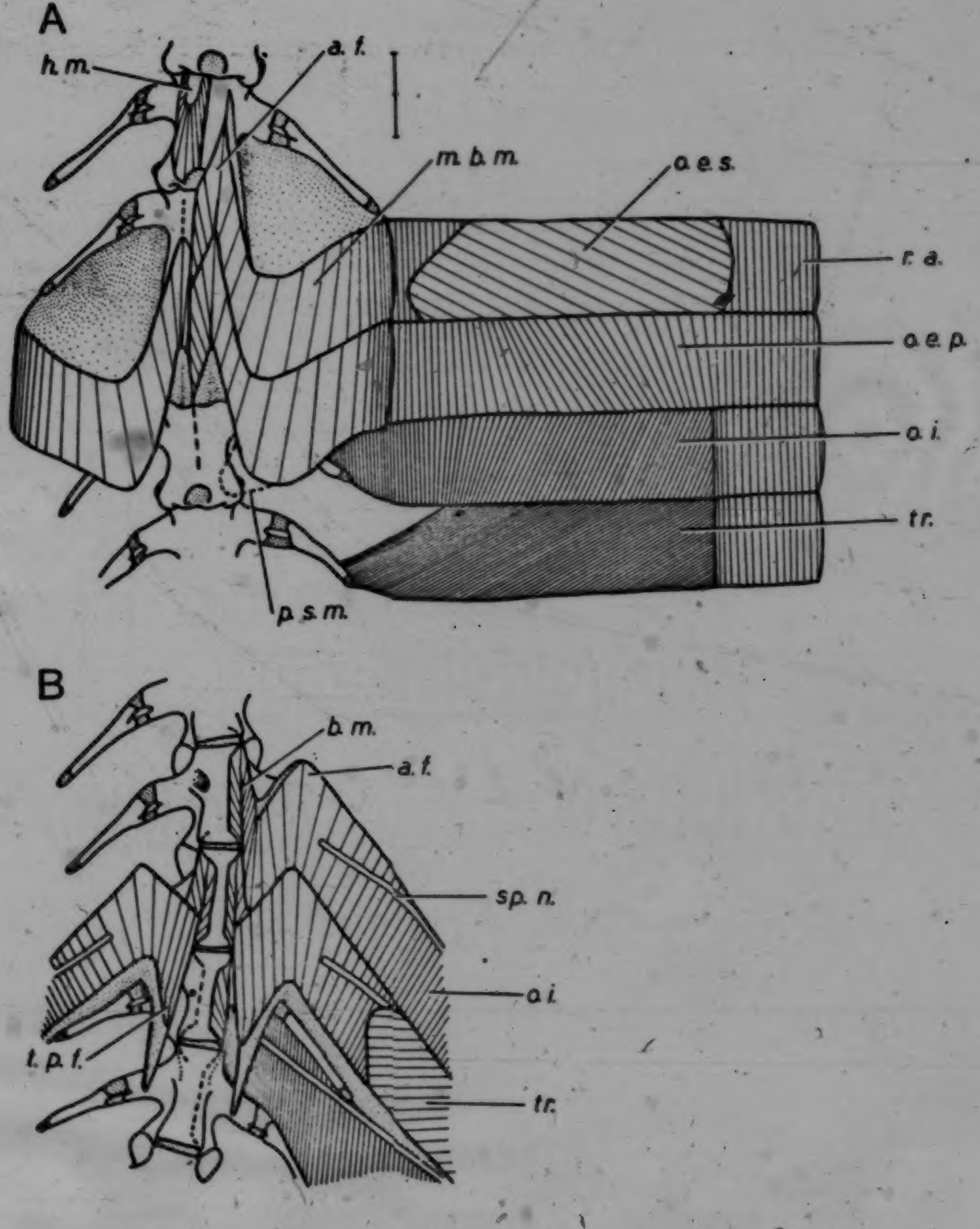
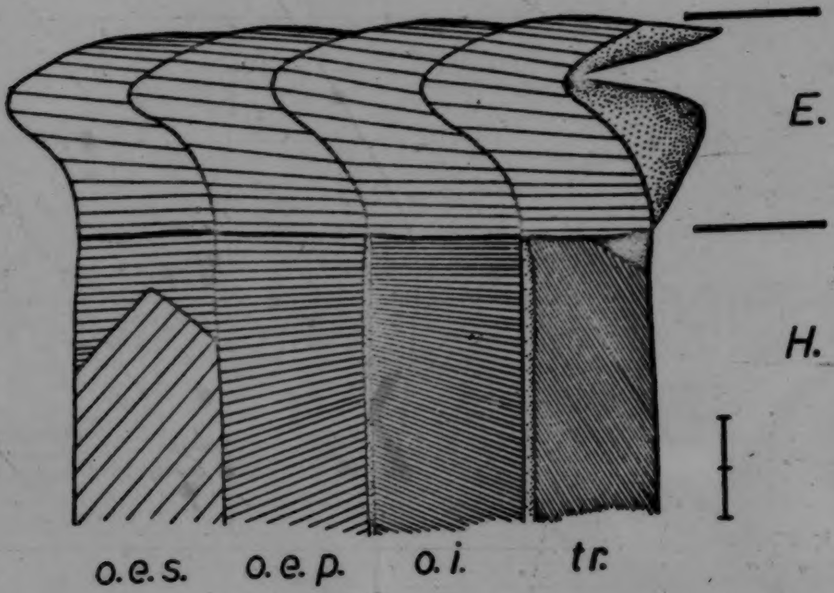

A
h.m.
a.f.
m.b.m.
a.e.s.
r.a.
a.e.p.
a.i.
tr.
p.s.m.
B
b.m.
a.f.
sp.n.
a.i.
t.p.f.
tr.

Figure 45. *Ambystoma tigrinum*: (A) lateral view of four segments of the trunk musculature; (B) trunk vertebrae in lateral view, showing position of the hyperapophyseal muscle; scales represent two millimeters; abbreviations given on pp. 4-7.

A


E.
H.
o.e.s.
o.e.p.
o.i.
tr.

B

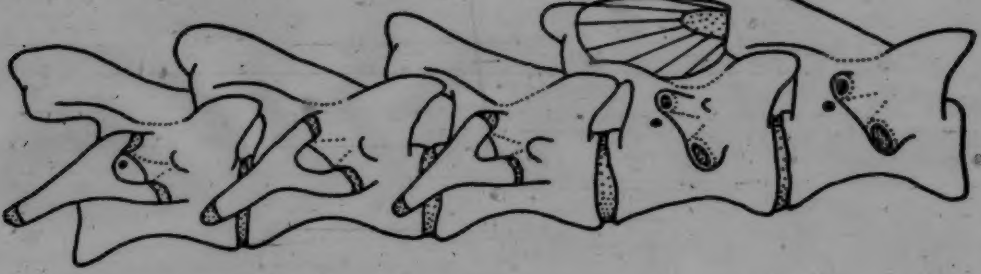


Figure 46. Dissection of *Necturus maculosus* with lateral abdominal musculature spread laterally: (A) dorsal view, lateral abdominal musculature not shown complete; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

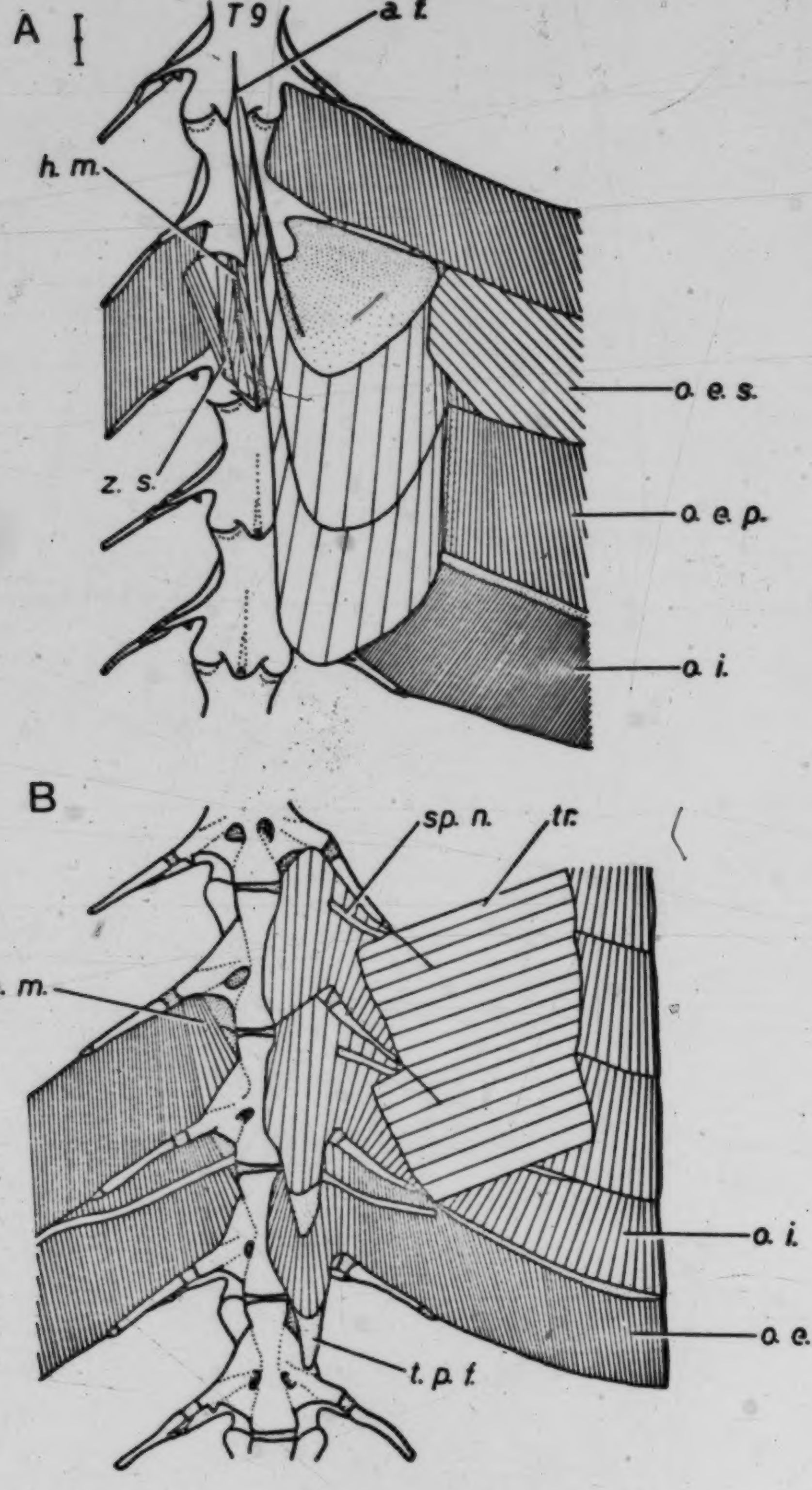

A
T9
a.t.
h.m.
z.s.
o.e.s.
o.e.p.
o.i.
B
sp.n.
tr.
t.p.m.
o.i.
o.e.p.
t.p.t.

Figure 47. Cross-sections through the trunk musculature of (A) *Cryptobranchus alleganiensis*; (B) *Necturus maculosus*; abbreviations given on pp. 4-7.

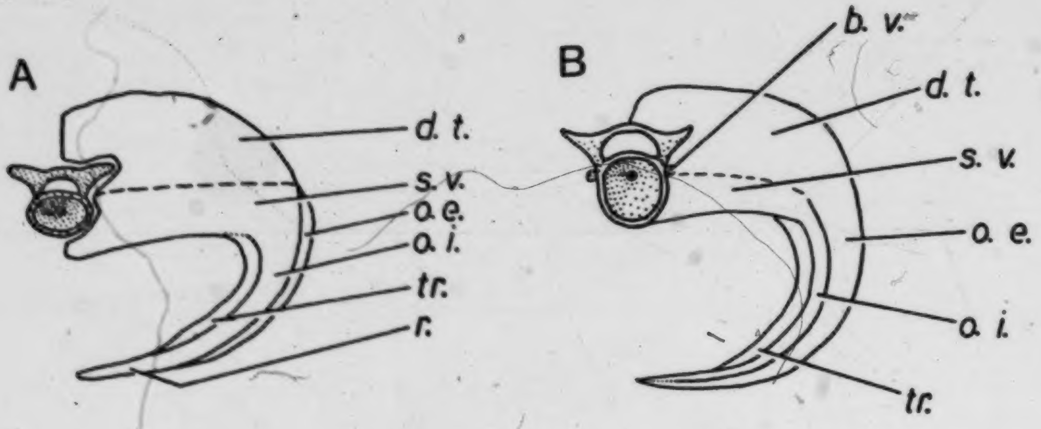

A
d. t.
s. v.
a. e.
a. i.
tr.
r.
B
b. v.
d. t.
s. v.
a. e.
a. i.
tr.

Figure 48. Partial dissection of the trunk musculature of *Proteus anguinus* in lateral view; scale represents two millimeters; abbreviations given on pp. 4-7.

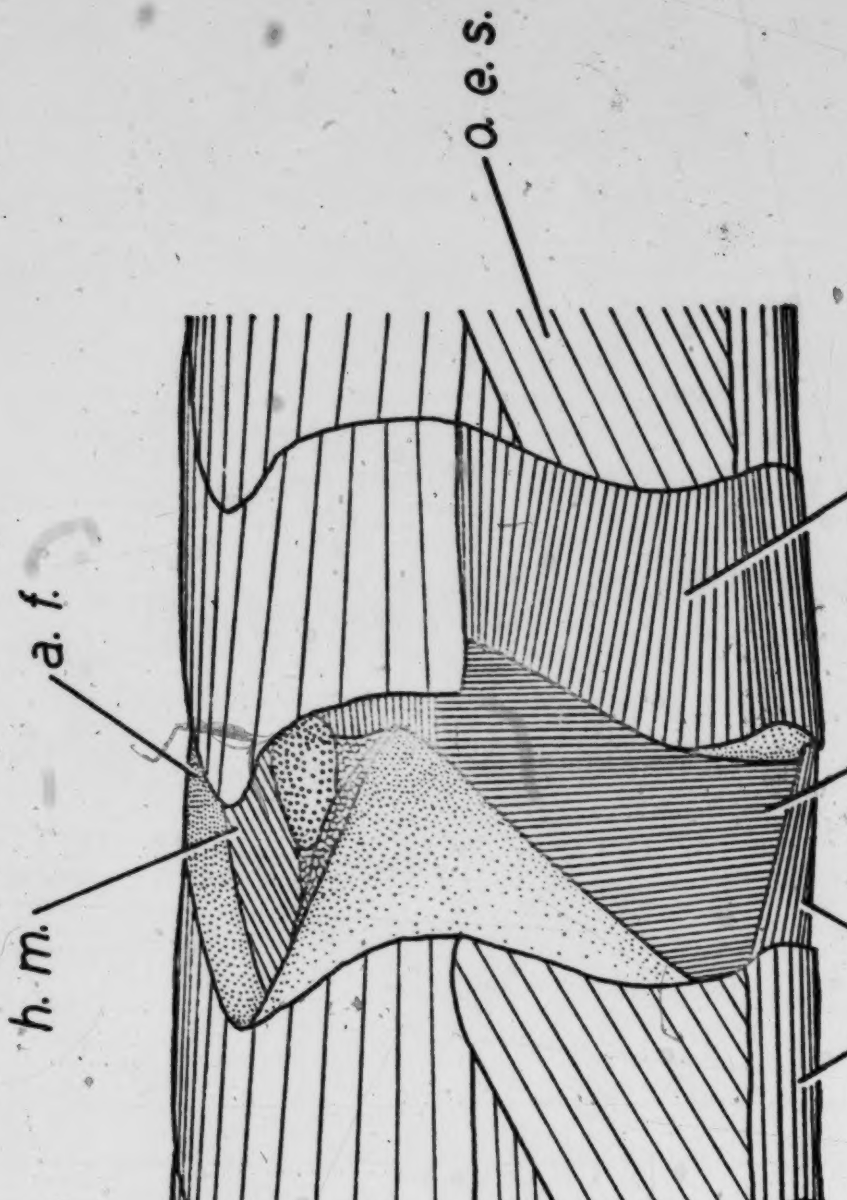

a. e. s.
o. i.
a. f.
tr.
h. m.
r. a.
r. l.

Figure 49. Dissection of *Plethodon jordani* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

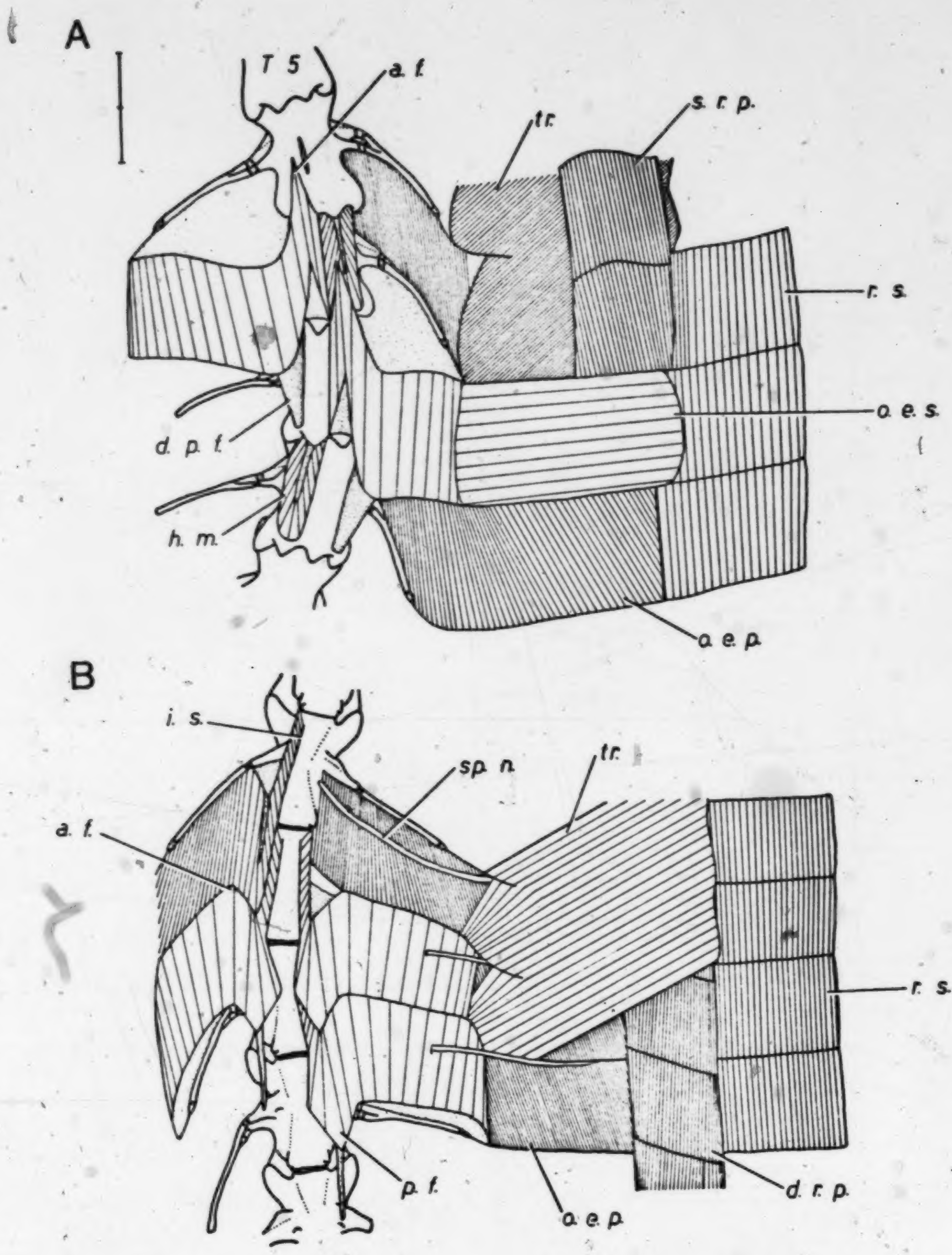

A
T 5
a. f.
tr.
s. r. p.
r. s.
a. e. s.
d. p. f.
h. m.
a. e. p.
B
i. s.
sp. n.
tr.
a. f.
r. s.
p. f.
a. e. p.
d. r. p.

Figure 50. Dissection of *Plethodon glutinosus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

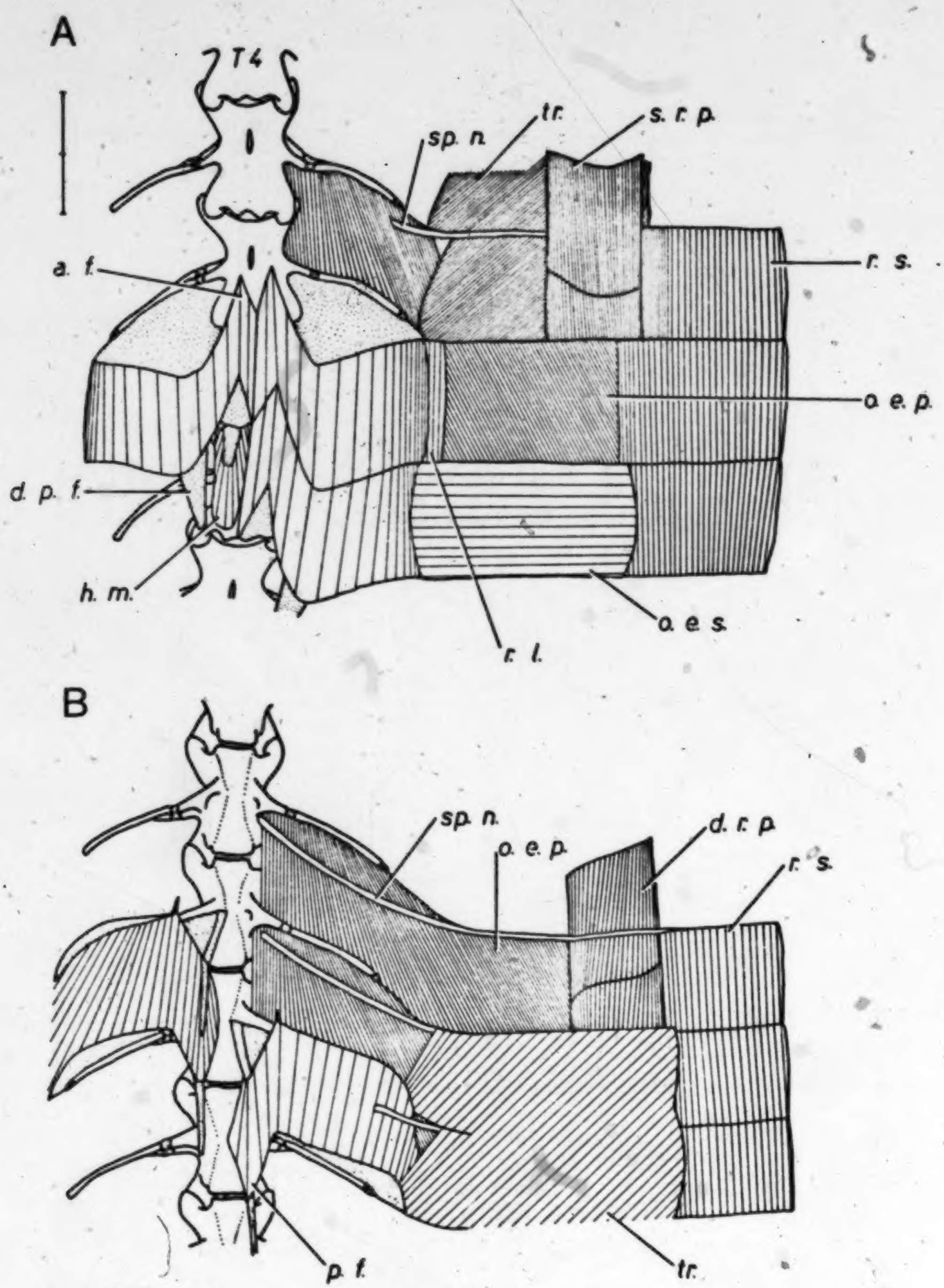

A
T4
sp. n.
tr.
s. r. p.
a. f.
r. s.
o. e. p.
d. p. f.
h. m.
o. e. s.
r. l.
B
sp. n.
d. r. p.
o. e. p.
r. s.
p. f.
tr.

Figure 51. Dissection of *Plethodon vehiculum* with lateral abdominal musculature not shown complete: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

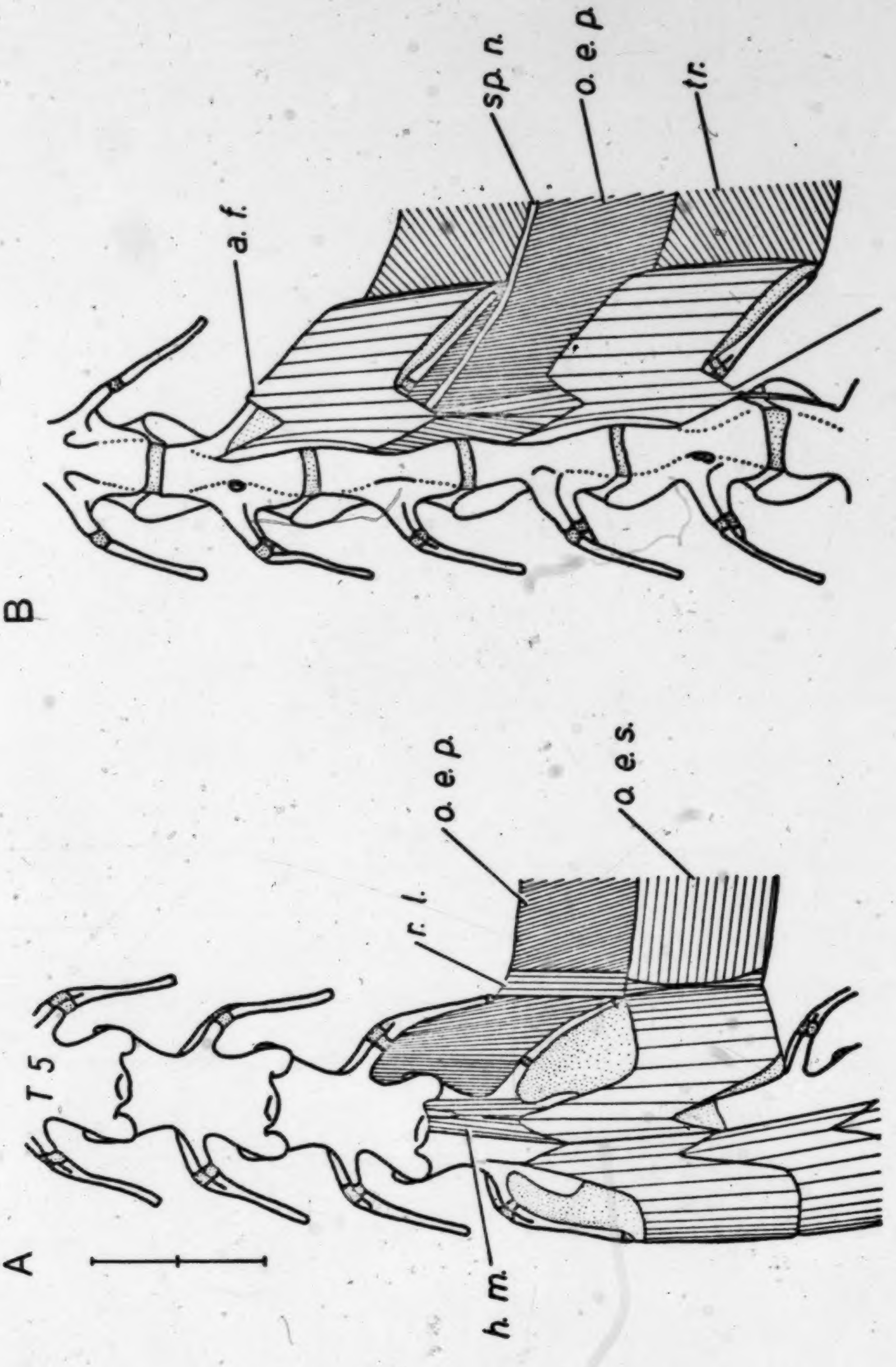

A
T 5
h. m.
r. l.
a. e. p.
a. e. s.
B
a. f.
sp. n.
a. e. p.
tr.

Figure 52. Dissection of *Plethodon neomexicanus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

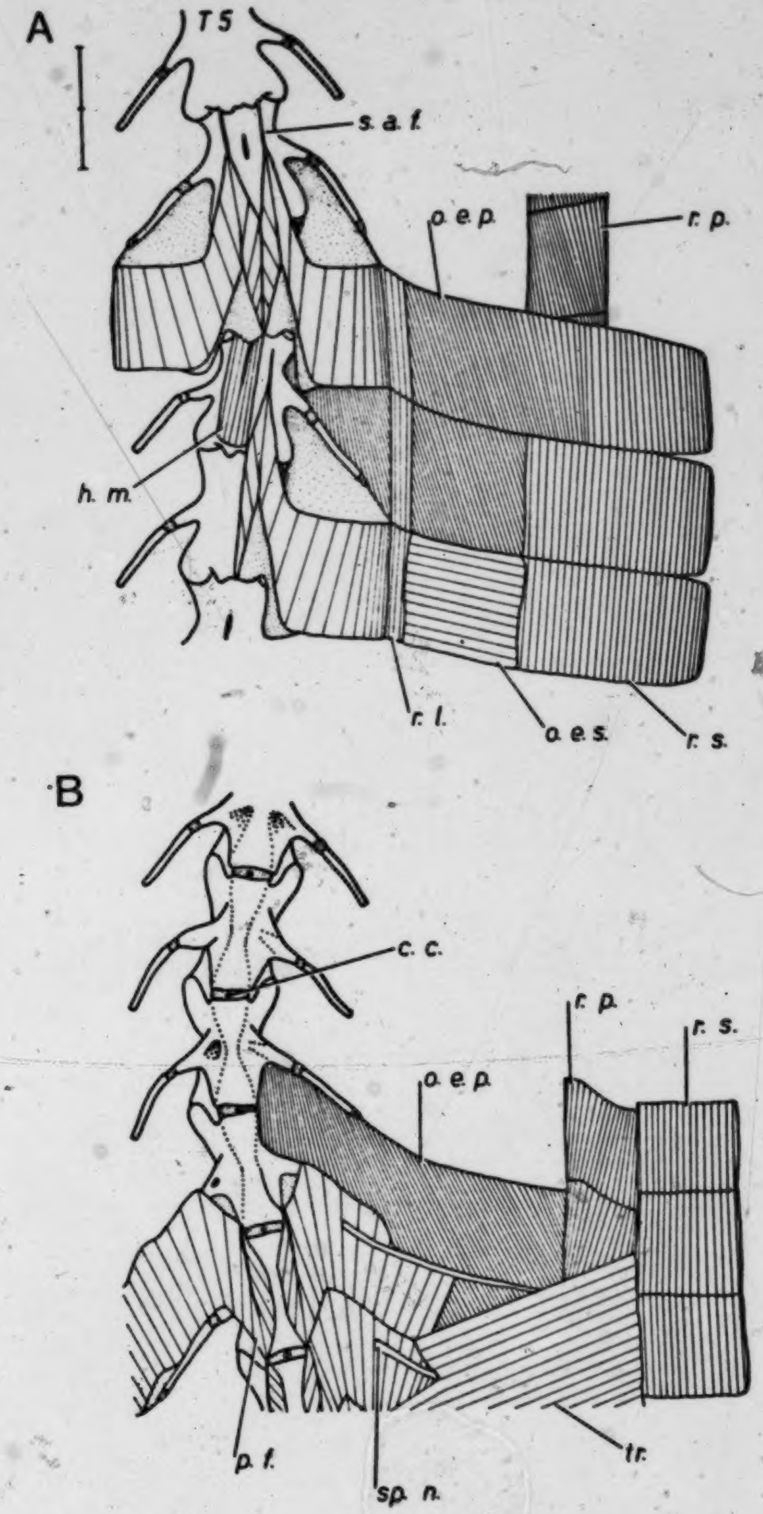

A
T5
s. a. f.
o. e. p.
r. p.
h. m.
r. l.
o. e. s.
r. s.
B
c. c.
r. p.
r. s.
o. e. p.
p. f.
sp. n.
tr.

Figure 53. Dissection of young *Ensatina eschscholtzii* (snout-vent length ca. 30 mm) with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

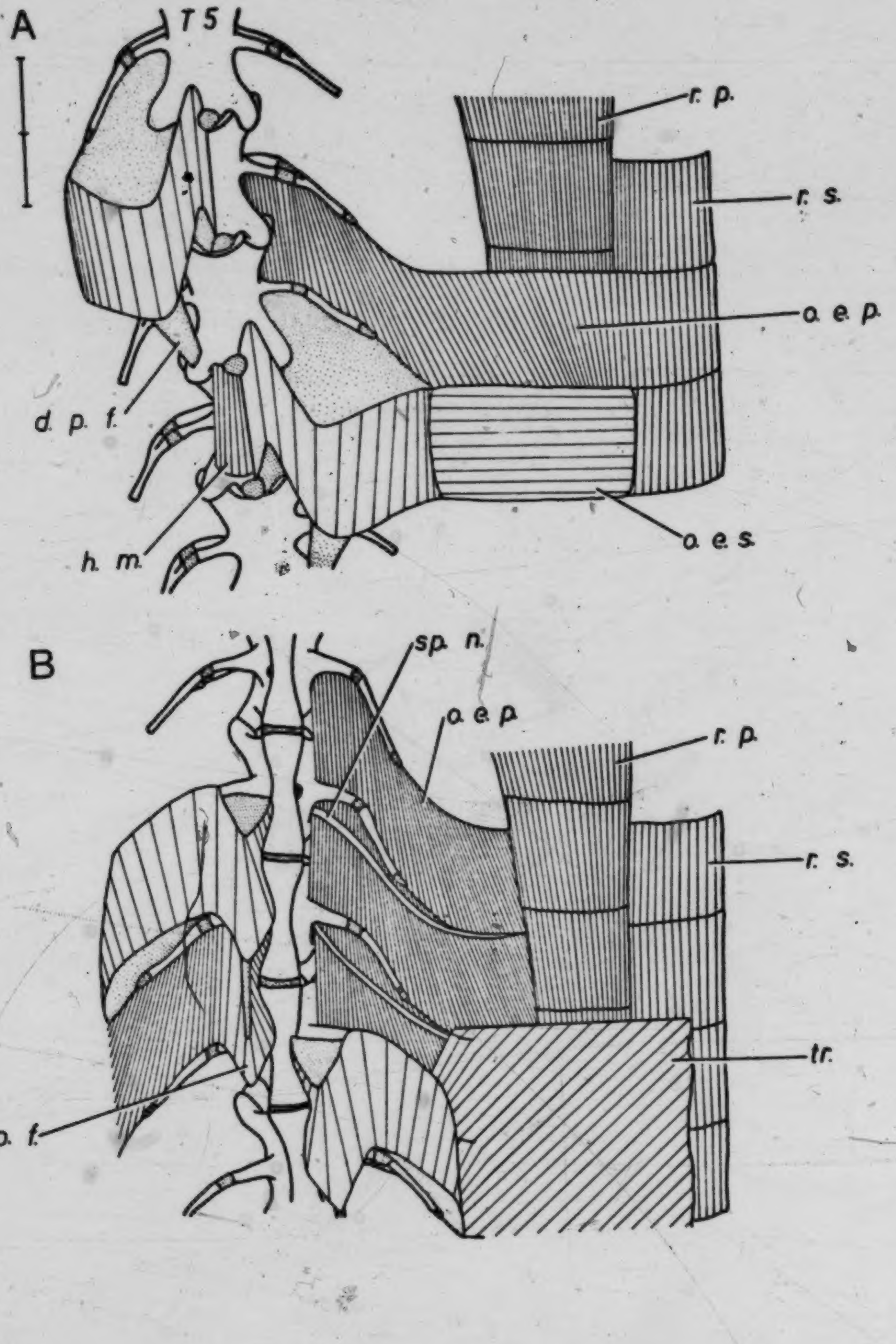
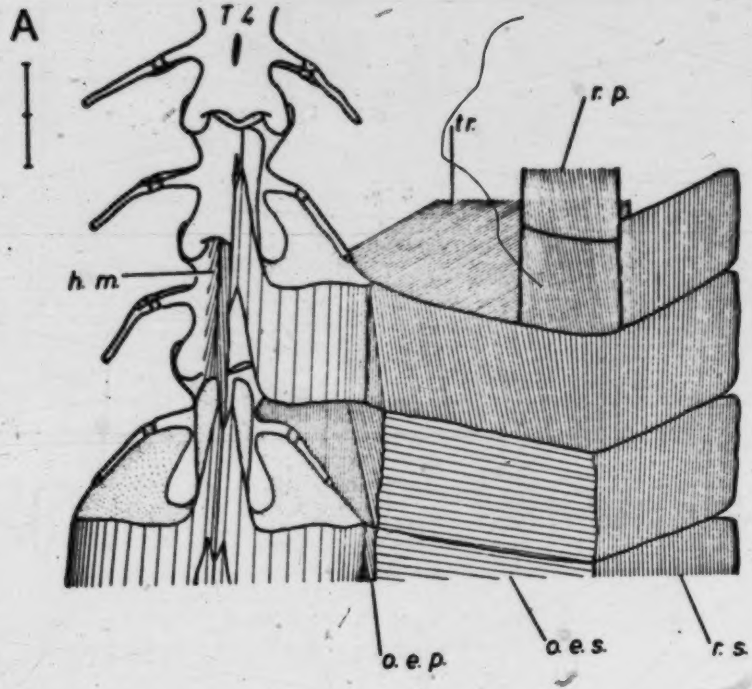

A
T5
r. p.
r. s.
a. e. p.
d. p. f.
h. m.
a. e. s.
B
sp. n.
a. e. p.
r. p.
r. s.
tr.
p. f.

Figure 54. Dissection of large adult *Ensatina eschscholtzii* with lateral abdominal musculature spread laterally; (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.


A
T 4
tr.
r. p.
h. m.
a. e. p.
a. e. s.
r. s.

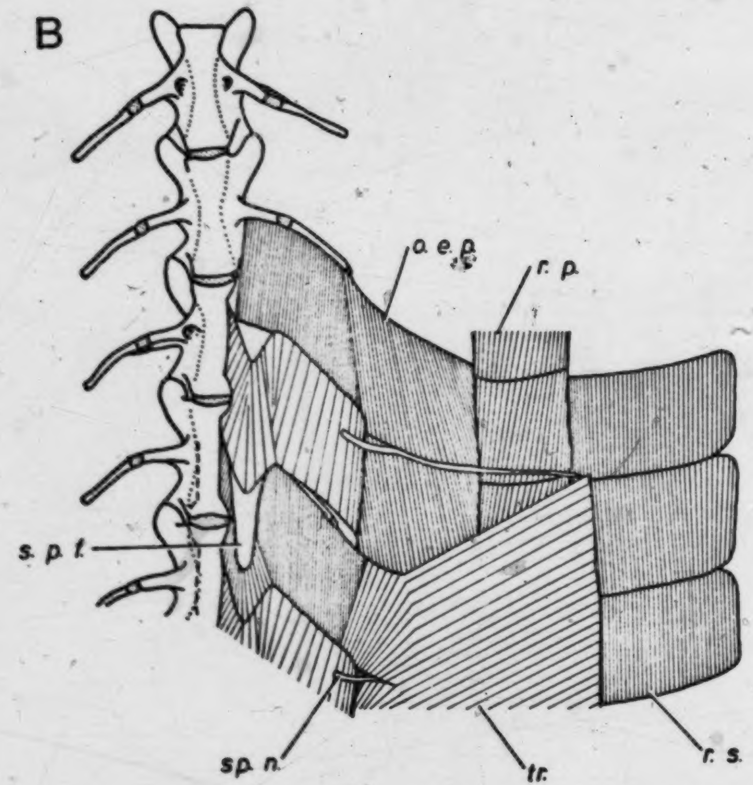

B
a. e. p.
r. p.
s. p. l.
sp. n.
tr.
r. s.

Figure 55. Dissection of *Aneides lugubris* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

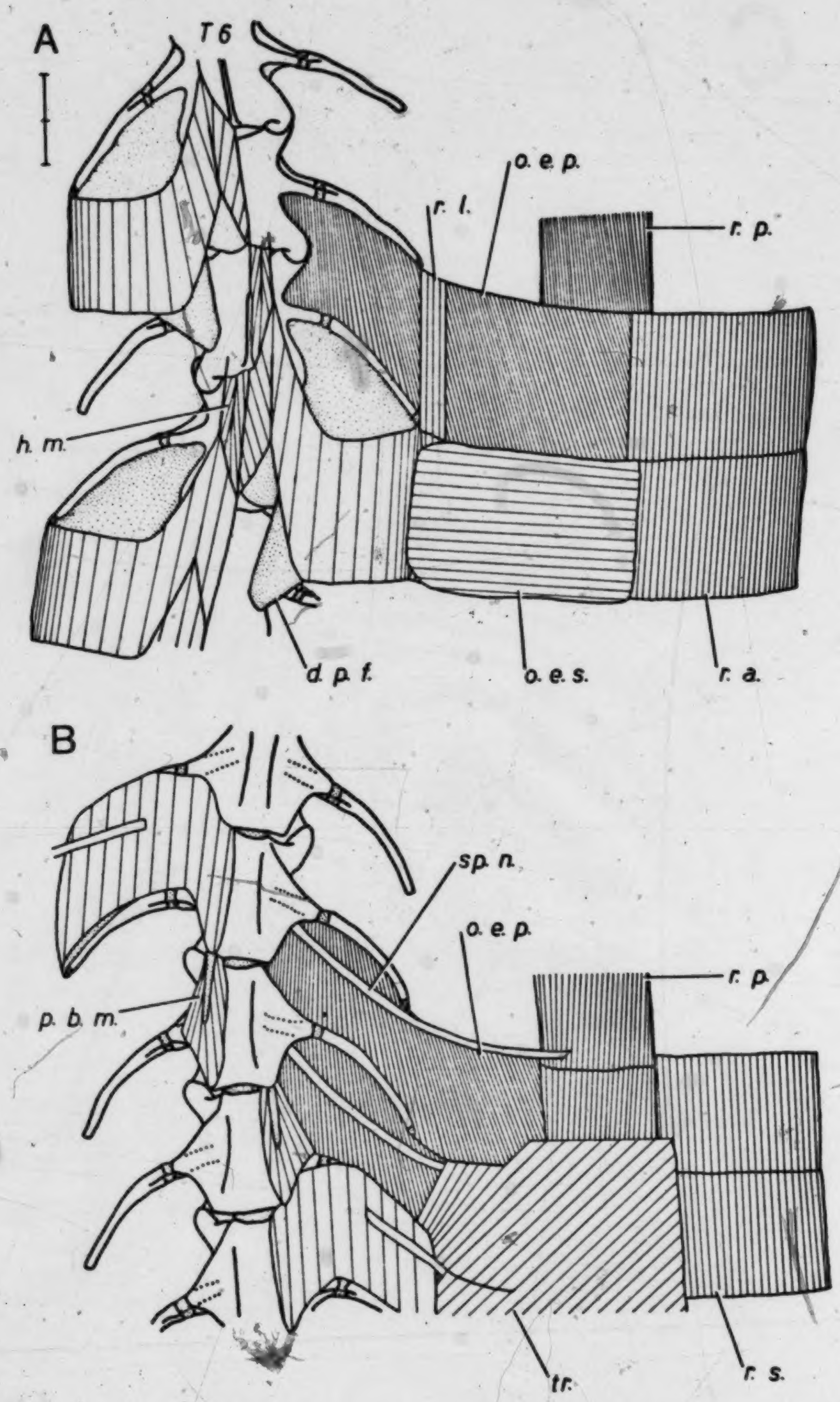

A
T6
o. e. p.
r. l.
r. p.
h. m.
d. p. f.
o. e. s.
r. a.
B
sp. n.
o. e. p.
r. p.
p. b. m.
tr.
r. s.

Figure 56. Dissection of *Hemidactylium scutatum* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents one millimeter; abbreviations given on pp. 4-7.

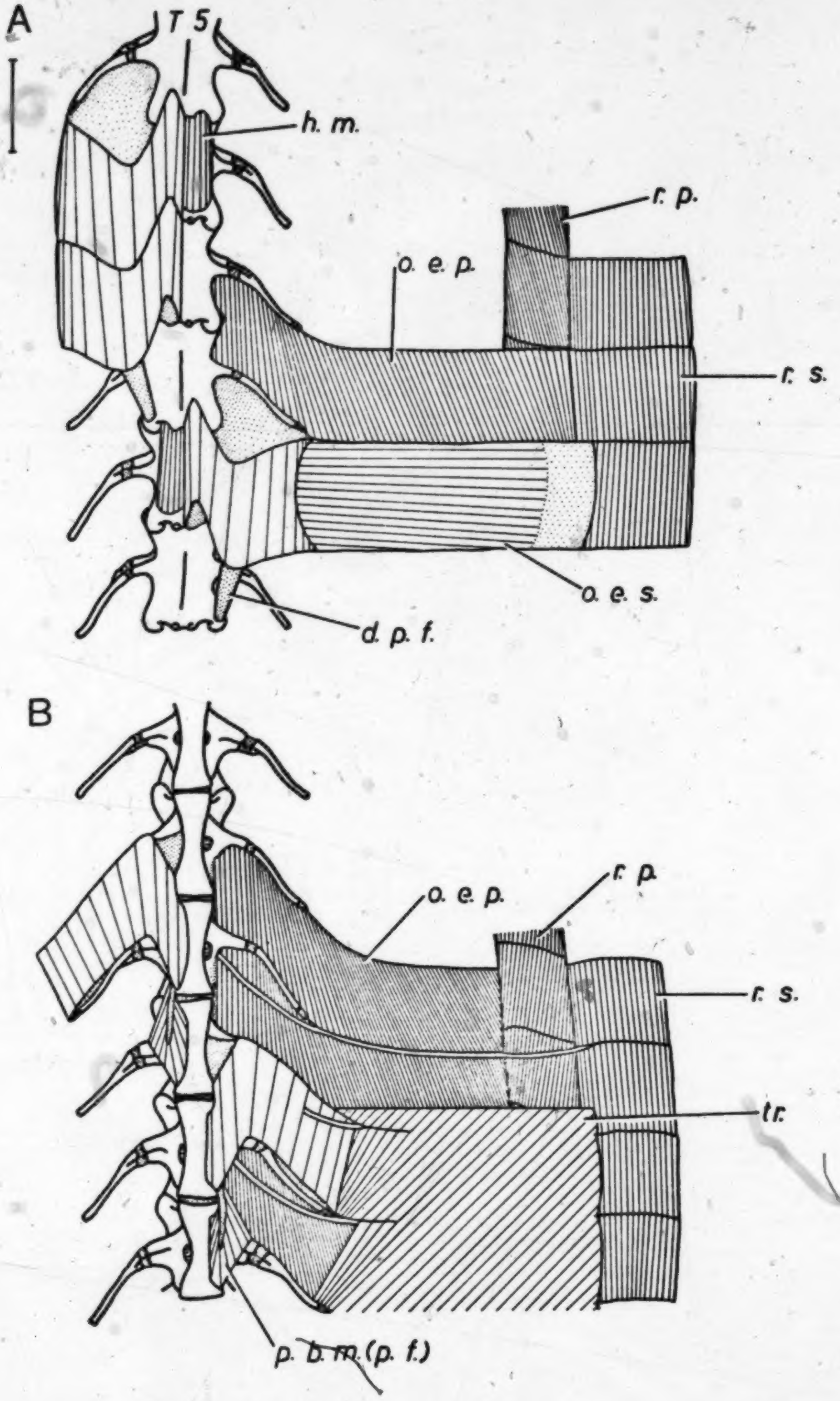

A
T 5
h. m.
r. p.
o. e. p.
r. s.
o. e. s.
d. p. f.
B
o. e. p.
r. p.
r. s.
tr.
p. b. m. (p. f.)

Figure 57. Dissection of *Batrachoseps attenuatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

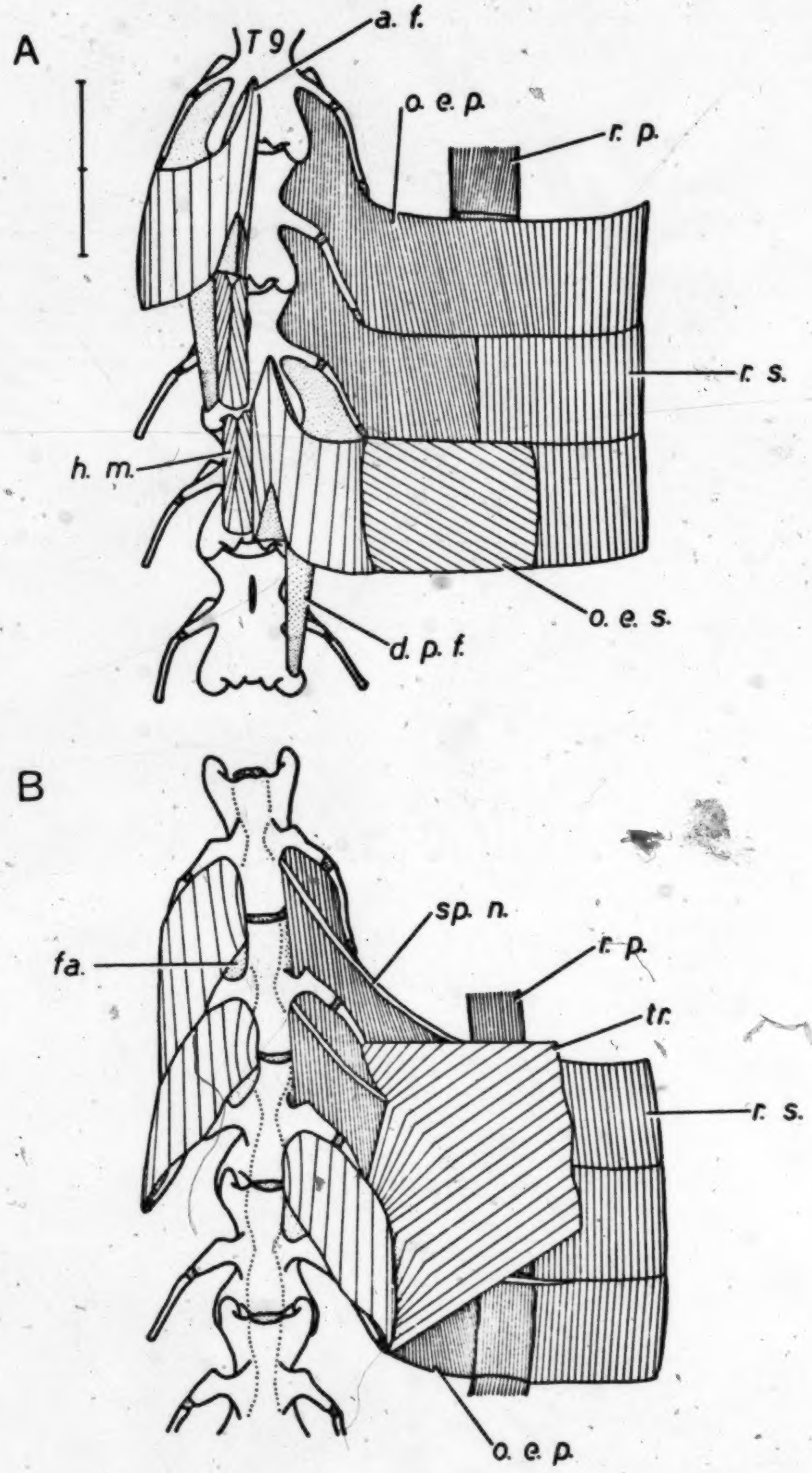

A
T 9
a. f.
o. e. p.
r. p.
r. s.
h. m.
o. e. s.
d. p. f.
B
sp. n.
r. p.
fa.
tr.
r. s.
o. e. p.

Figure 58. Dissection of *Bolitoglossa subpalmata* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

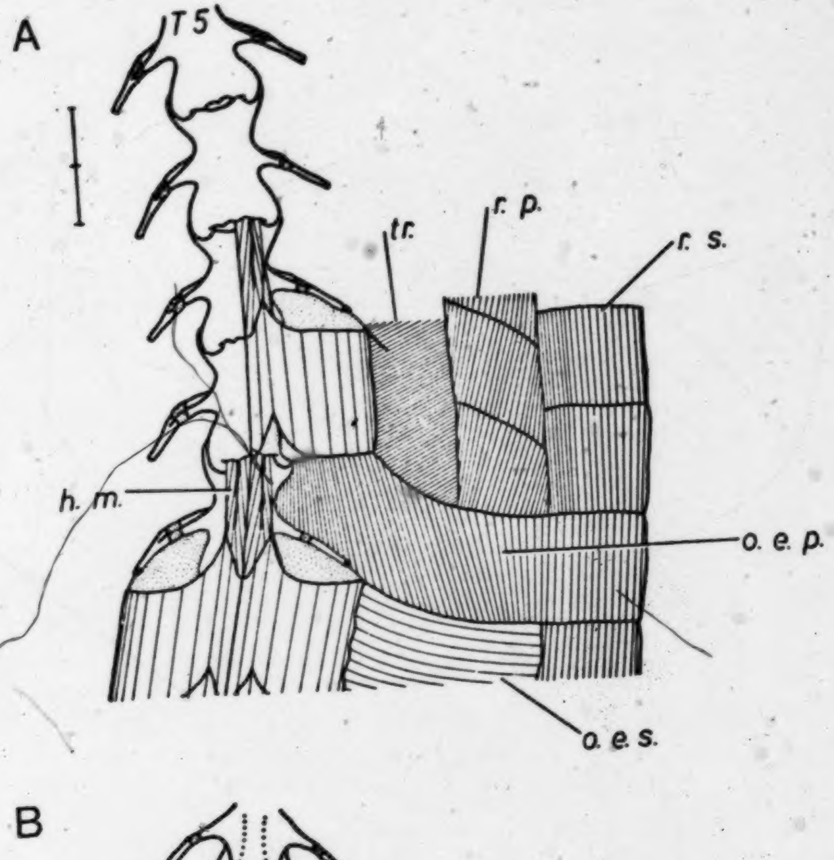

A
T5
tr.
r. p.
r. s.
h. m.
o. e. p.
o. e. s.
B
o. e. p.
r. p.
r. s.
s. p. f.
tr.
sp. n.

Figure 59. Dissection of *Pseudoeurycea cephalica* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

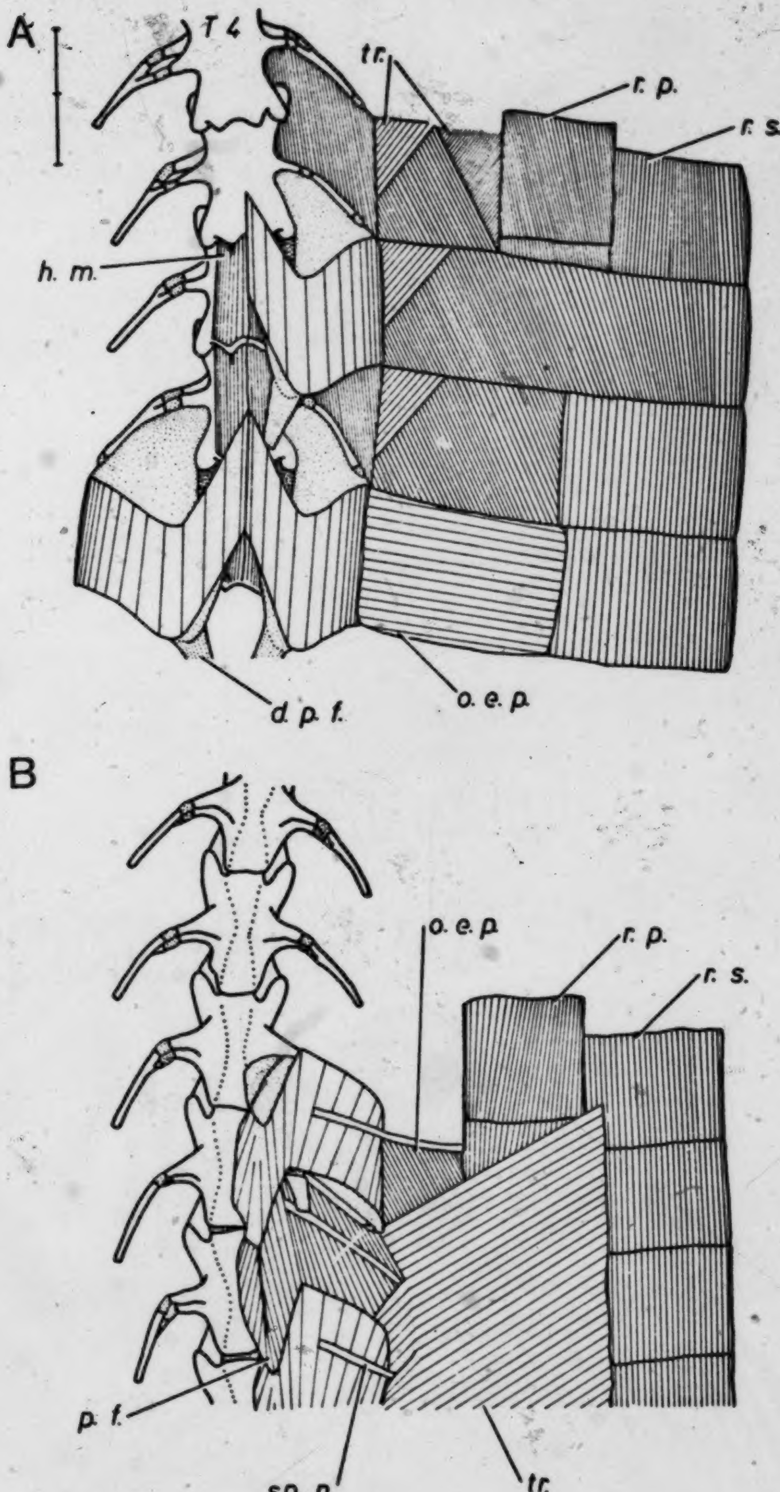

A
T 4
tr.
r. p.
r. s.
h. m.
d. p. f.
o. e. p.
B
o. e. p.
r. p.
r. s.
p. f.
sp. n.
tr.

Figure 60. Dissection of *Chiropterotriton chiroptera* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

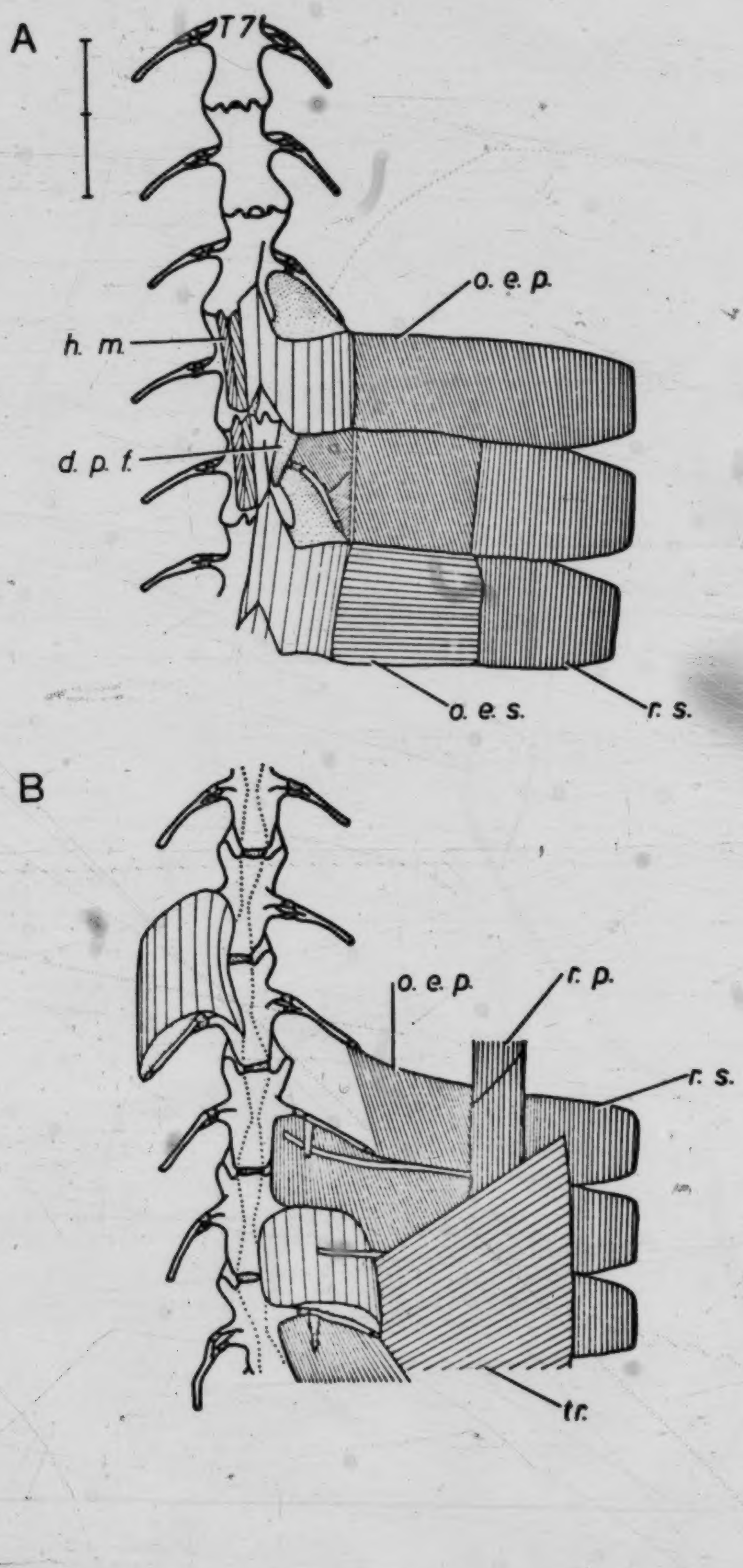

A
T7
o. e. p.
h. m.
d. p. f.
o. e. s.
r. s.
B
o. e. p.
r. p.
r. s.
tr.

Figure 61. Dissection of *Eurycea bislineata* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents one millimeter; abbreviations given on pp. 4-7.

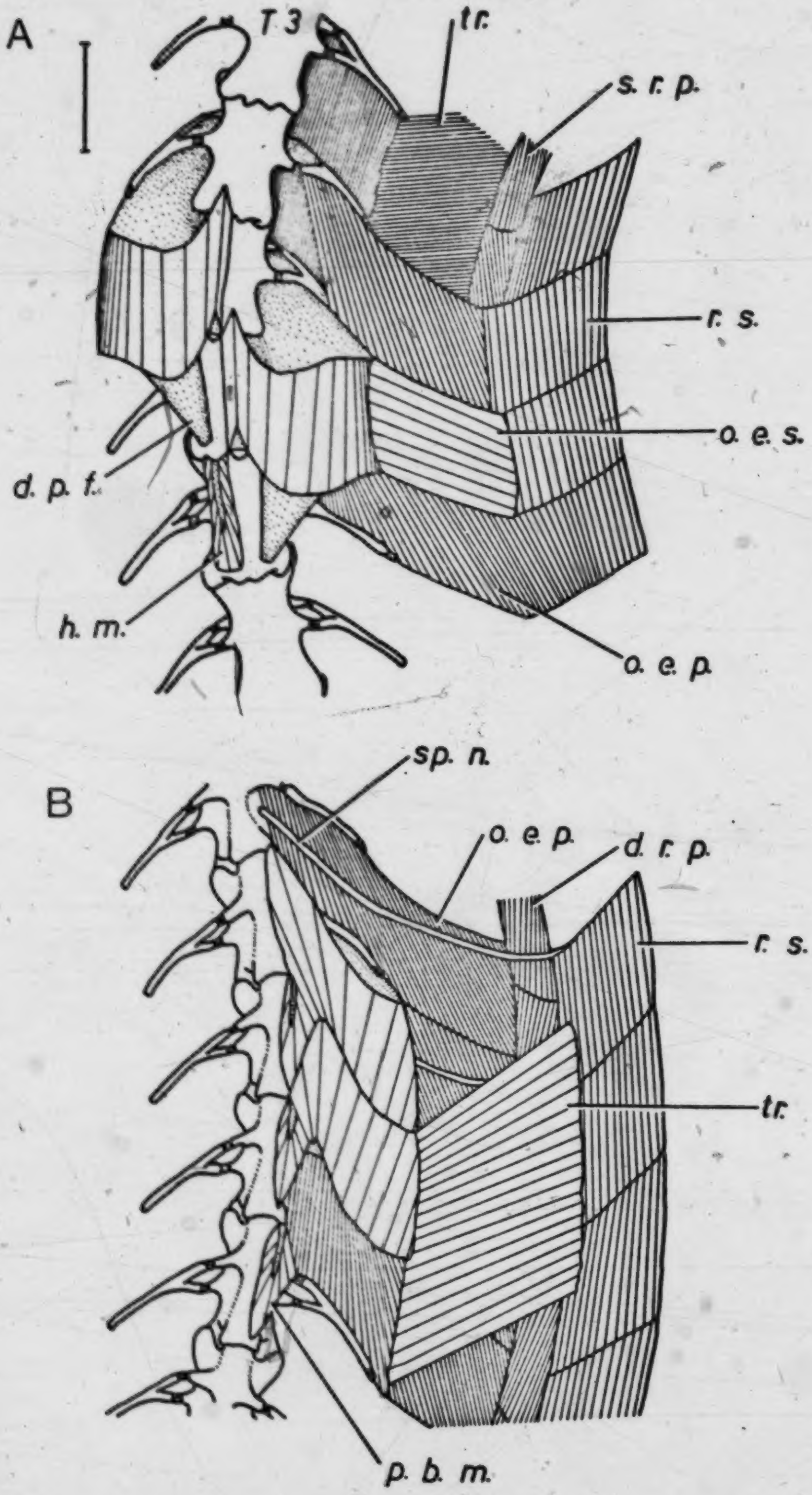

A
T 3
tr.
s. r. p.
r. s.
o. e. s.
d. p. f.
h. m.
o. e. p.
B
sp. n.
o. e. p.
d. r. p.
r. s.
tr.
p. b. m.

Figure 62. Dissection of *Eurycea quadridigitata* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents one millimeter; abbreviations given on pp. 4-7.

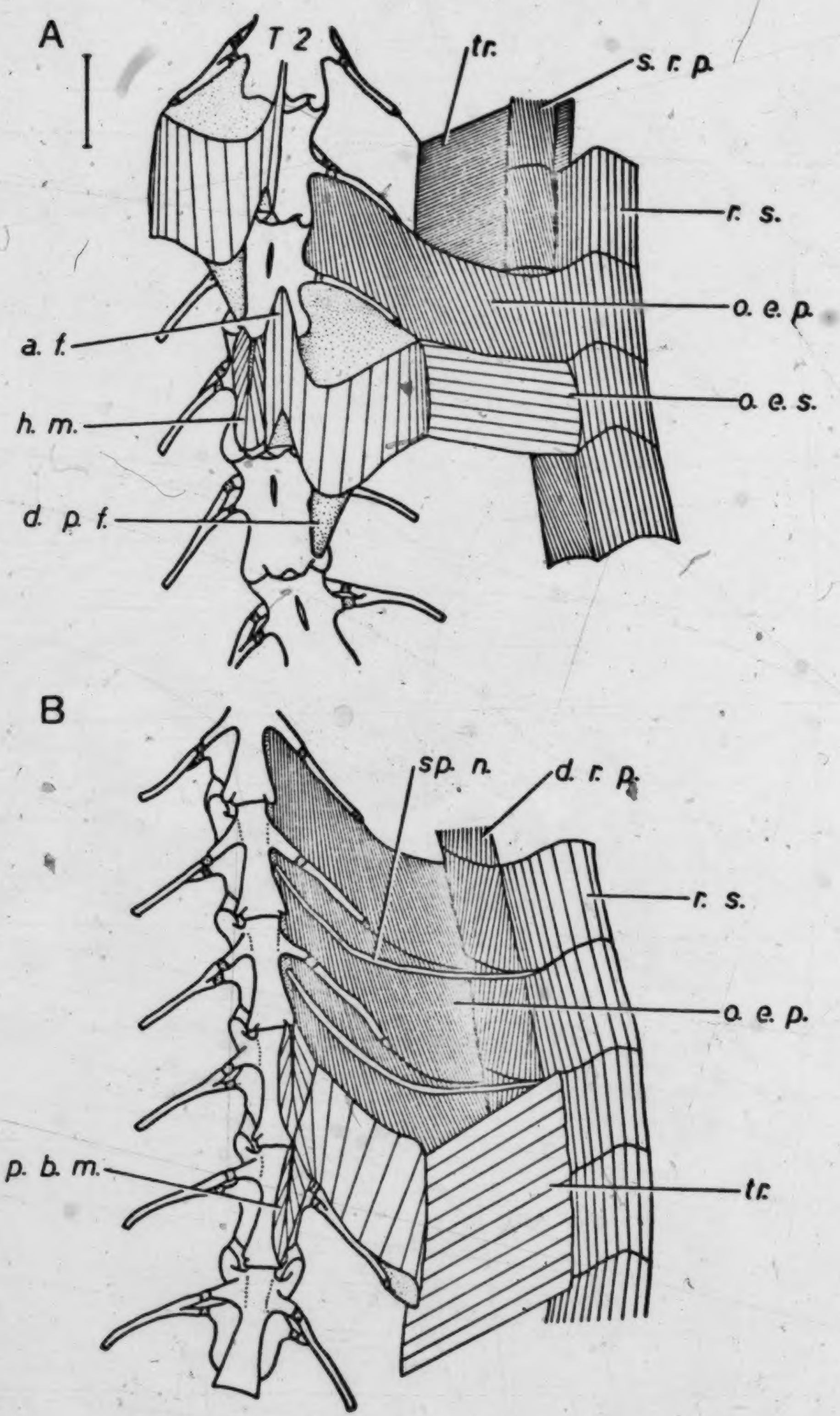

A
T 2
tr.
s. r. p.
r. s.
o. e. p.
a. f.
o. e. s.
h. m.
d. p. f.
B
sp. n.
d. r. p.
r. s.
o. e. p.
p. b. m.
tr.

Figure 63. Dissection of *Typhlotriton spelaeus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

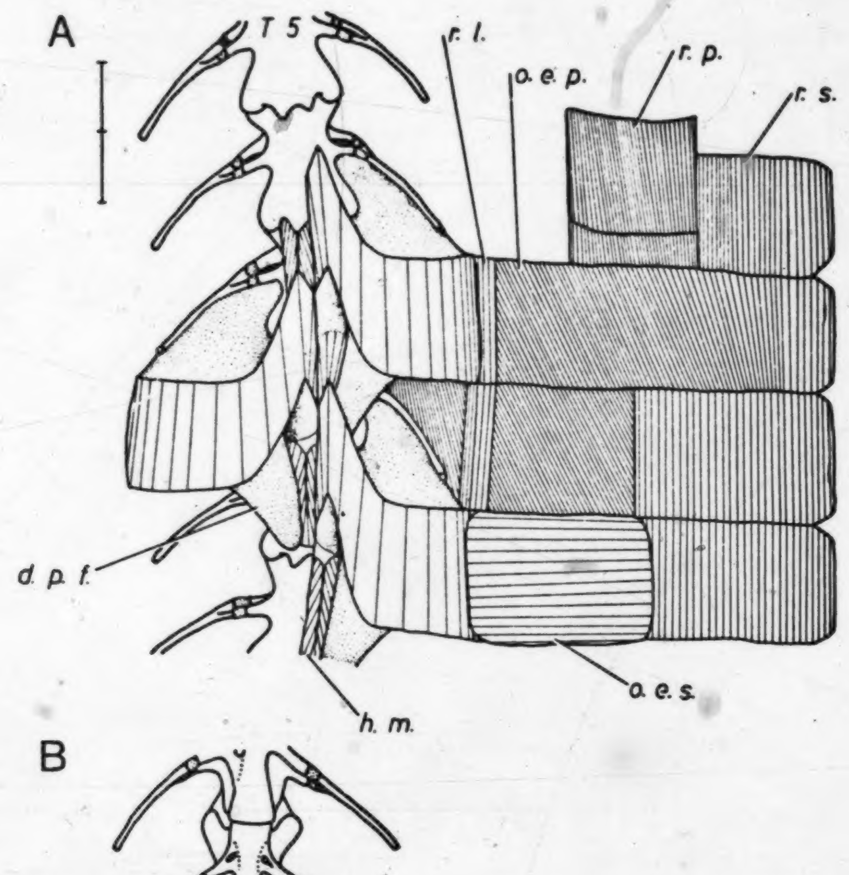

A
T 5
r. l.
a. e. p.
r. p.
r. s.
d. p. f.
a. e. s.
h. m.
B
a. e. p.
r. p.
r. s.
sp. n.
p. b. m.
tr.

Figure 64. Dissection of *Stereochilus marginatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

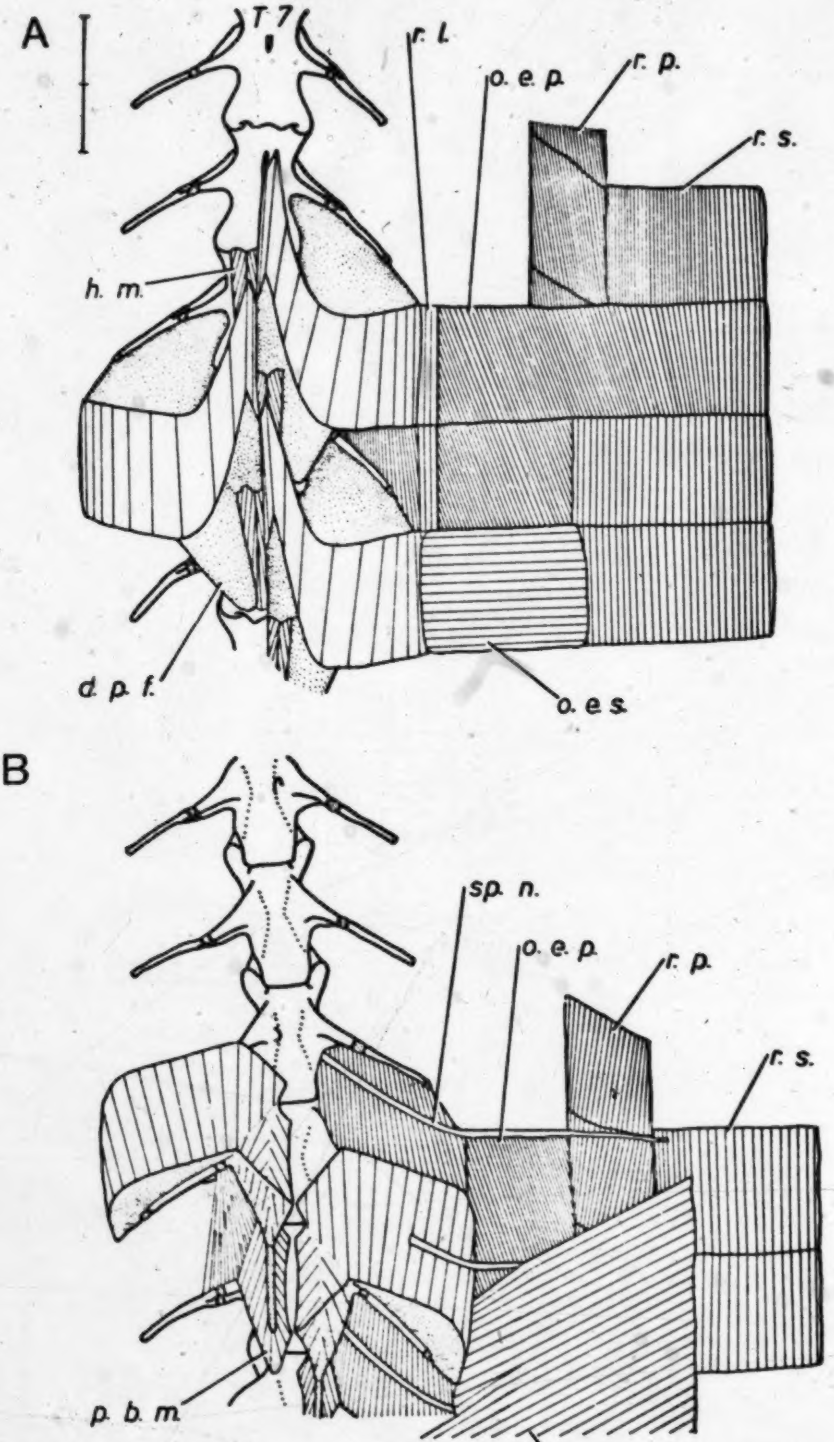

A
T 7
r. l.
o. e. p.
r. p.
r. s.
h. m.
d. p. f.
o. e. s.
B
sp. n.
o. e. p.
r. p.
r. s.
p. b. m.
tr.

Figure 65. Dissection of *Gyrinophilus porphyriticus* with lateral abdominal musculature spread laterally: (A) dorsal view, a small *rectus lateralis* is present but not figured; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

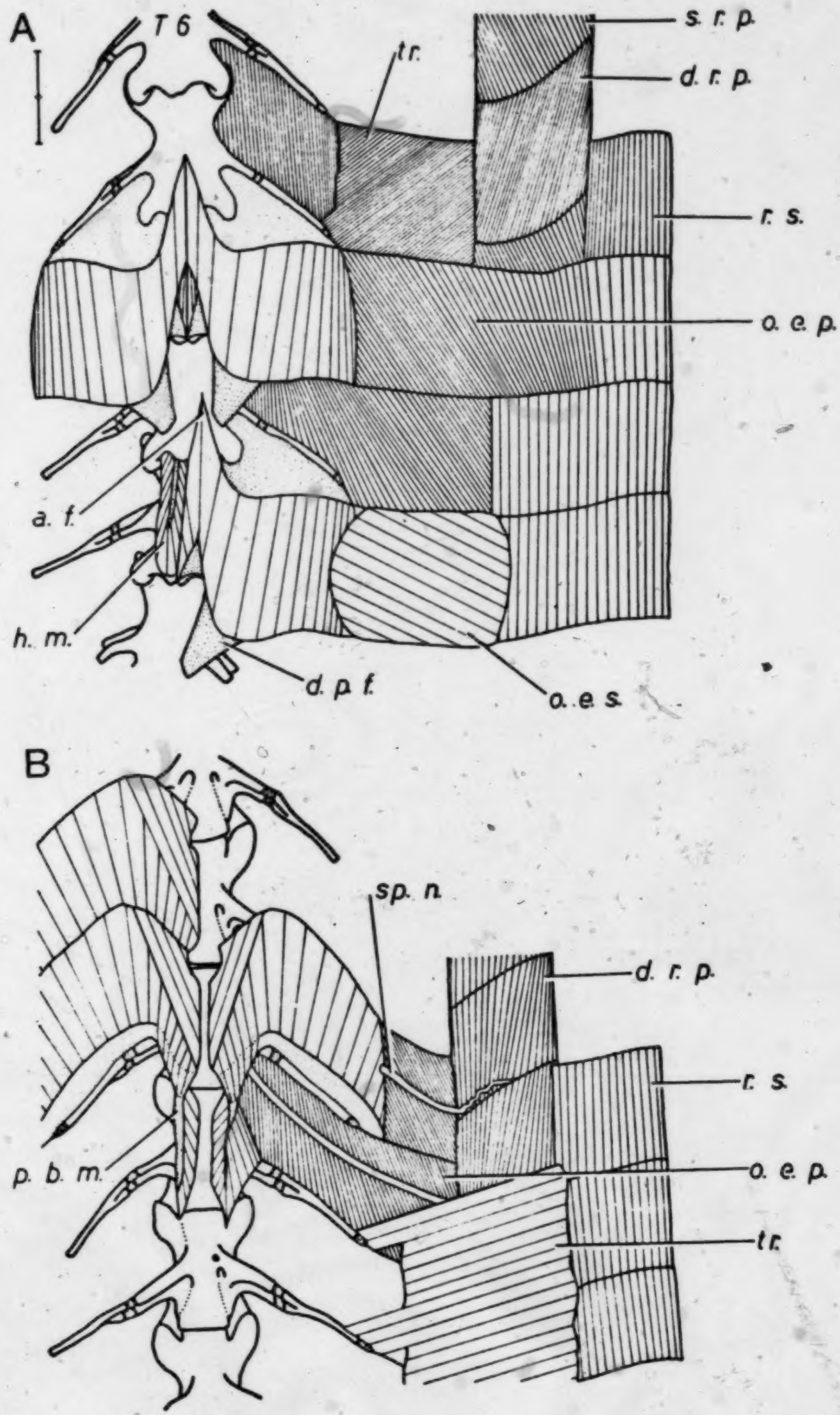

A
T6
tr.
s. r. p.
d. r. p.
r. s.
o. e. p.
a. f.
h. m.
d. p. f.
o. e. s.
B
sp. n.
d. r. p.
r. s.
p. b. m.
o. e. p.
tr.

Figure 66. Dissection of *Pseudotriton ruber* with lateral abdominal musculature spread laterally: (A) dorsal view, a small, ill-defined *rectus lateralis* is present but not figured; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

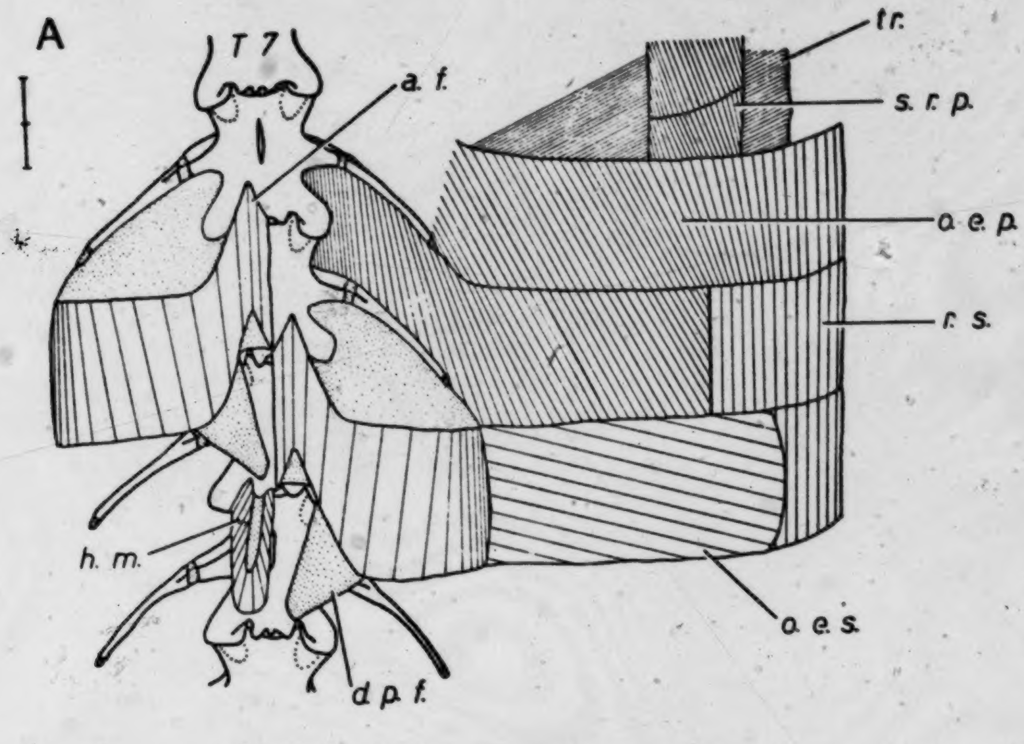

A
T 7
a. f.
tr.
s. r. p.
o. e. p.
r. s.
h. m.
o. e. s.
d. p. f.
B
sp. n.
tr.
d. p. f.
r. s.
p. b. m.
s. r. p.
o. e. p.
d. r. p.

Figure 67. Dissection of *Desmognathus fuscus* with lateral abdominal musculature spread laterally: (A) dorsal view; (b) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

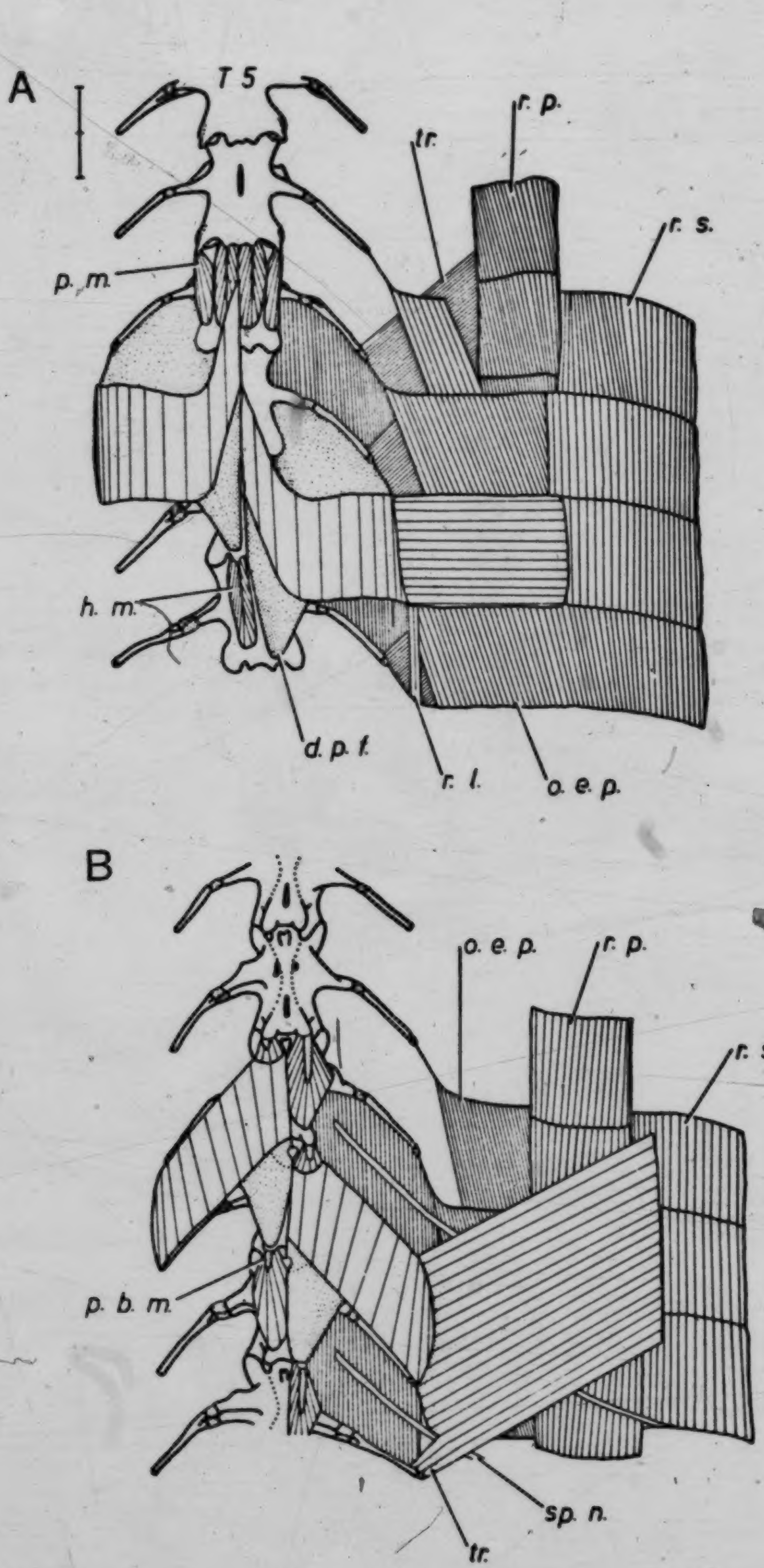
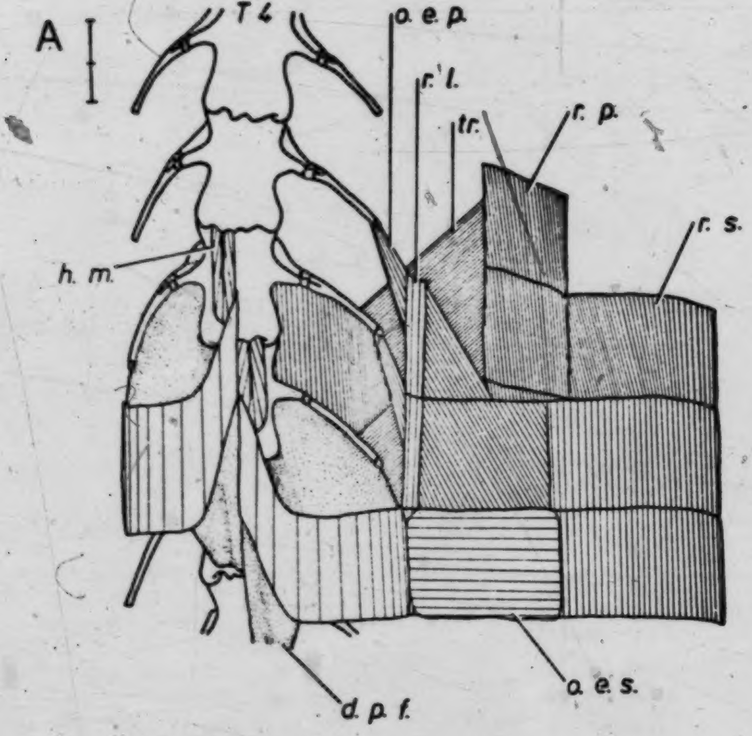

A
T 5
r. p.
tr.
r. s.
p. m.
h. m.
d. p. f.
r. l.
o. e. p.
B
o. e. p.
r. p.
r. s.
p. b. m.
sp. n.
tr.

Figure 68. Dissection of *Leurognathus marmoratus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

A


T 4
o. e. p.
r.' l.
tr.
r. p.
r. s.
h. m.
d. p. f.
o. e. s.

B

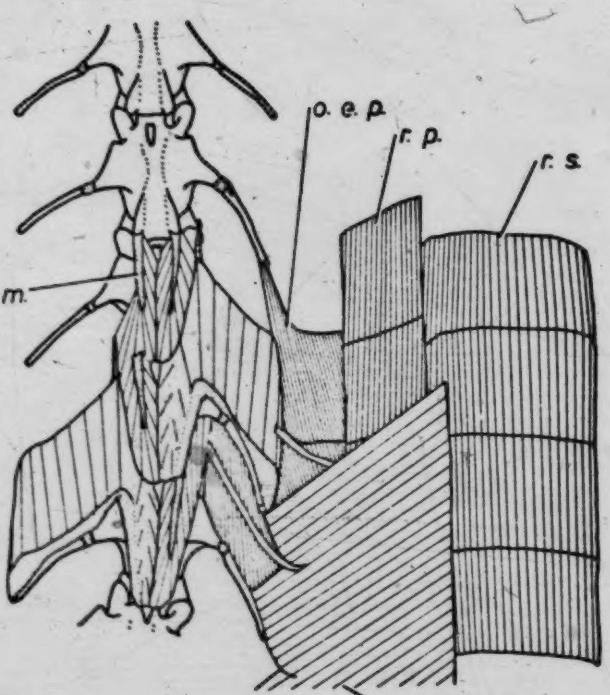

o. e. p.
r. p.
r. s.
p. b. m.
tr.

Figure 69. Dissection of *Salamandra salamandra* with lateral abdominal musculature spread laterally: (A) dorsal view, displacement of anterior flexures by the dorsal glands not shown; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

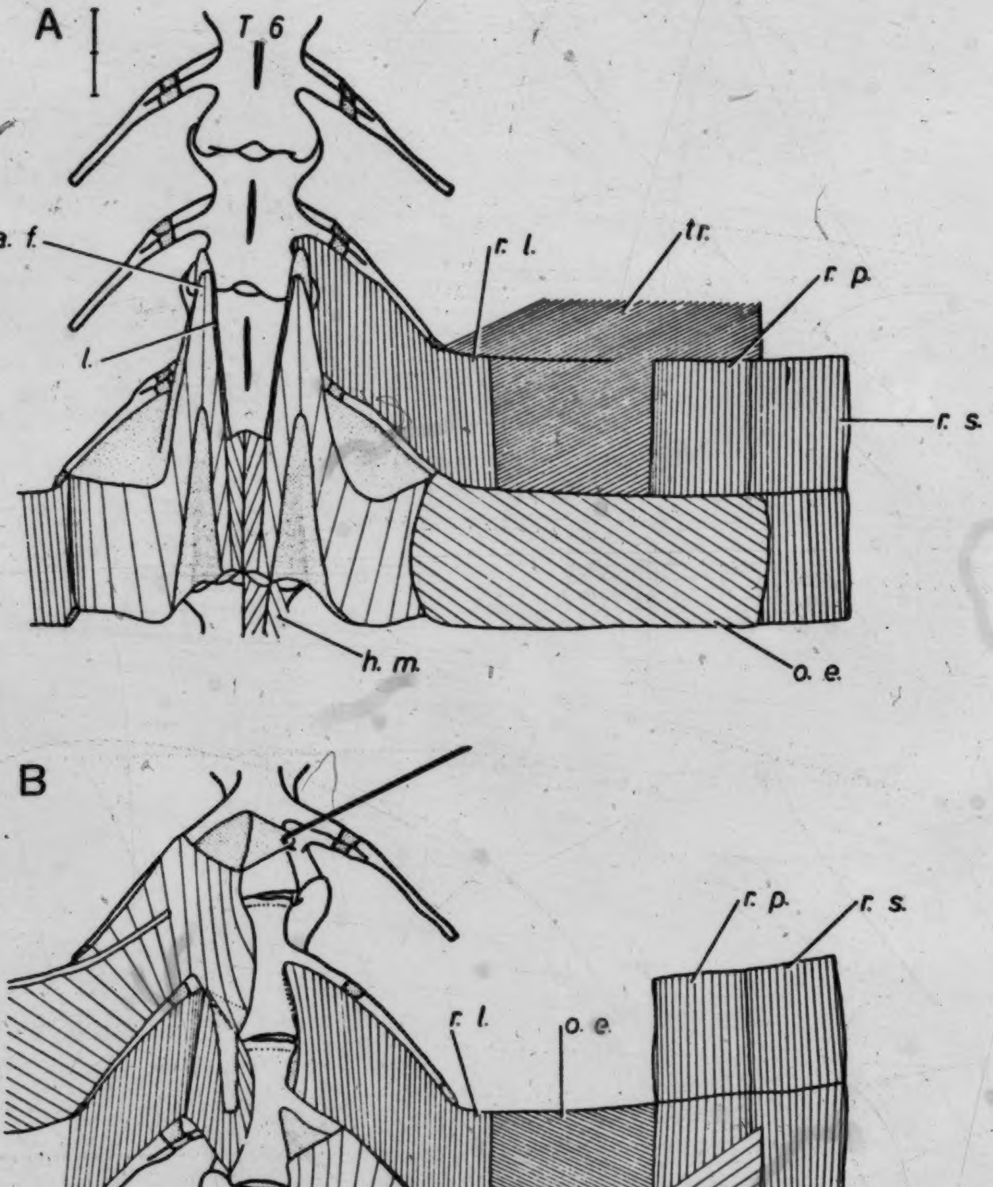

A
T 6
a. f.
l.
r. l.
tr.
r. p.
r. s.
h. m.
o. e.
B
r. p.
r. s.
r. l.
o. e.
tr.
sp. n.
p. f.
p. b. m.

Figure 70. *Salamandra salamandra*: camera lucida sketch of vertebrae from the midtrunk of a juvenile to show the position of the paired poison glands with respect to the column.

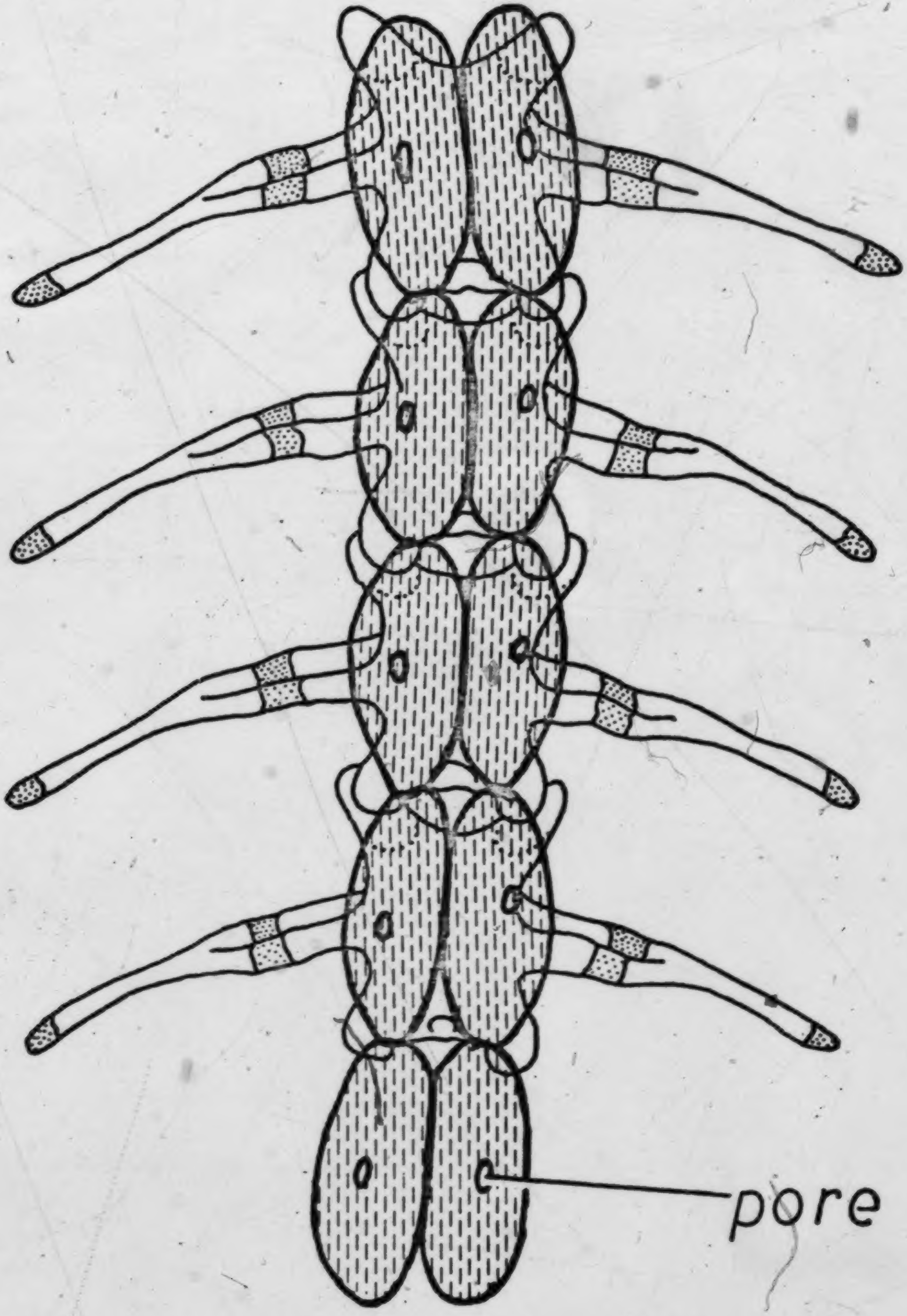

pore

Figure 71. Dissection of *Pleurodeles waltli* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

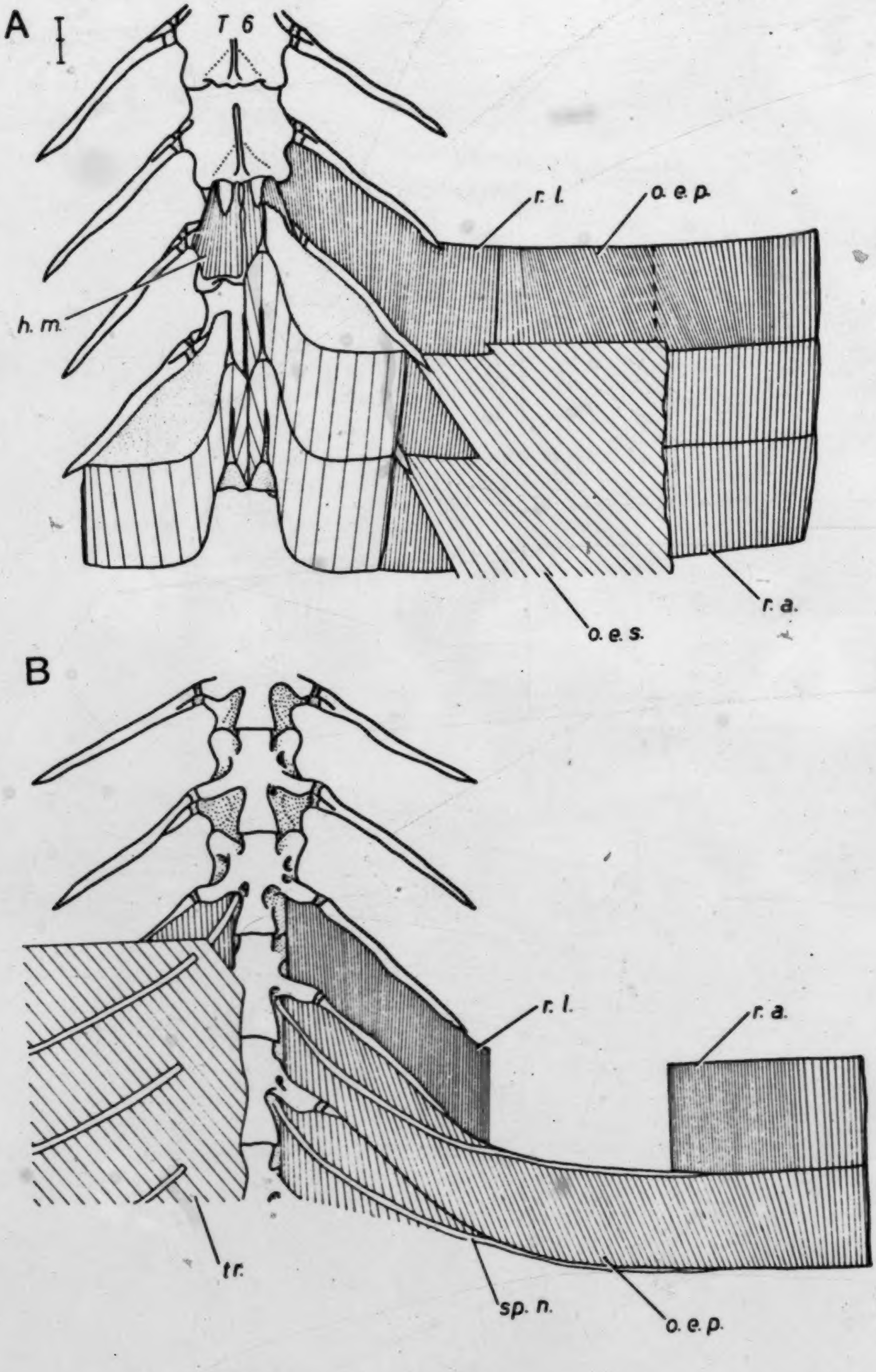

A
T 6
r. l.
o. e. p.
h. m.
o. e. s.
r. a.
B
r. l.
r. a.
tr.
sp. n.
o. e. p.

Figure 72. Dissection of *Salamandrina terdigitata* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

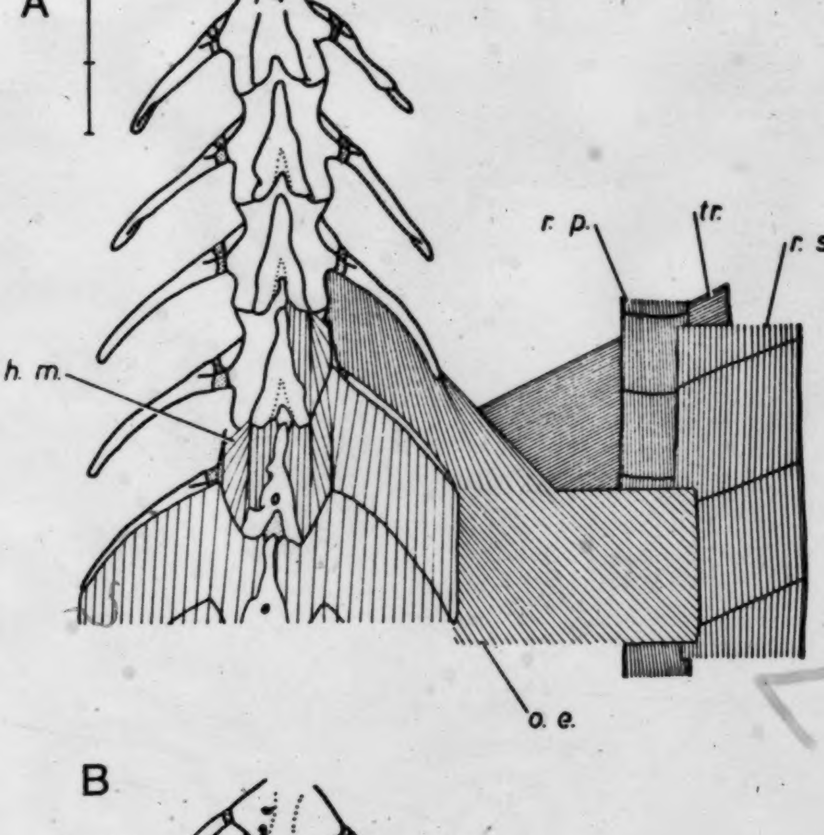

A
T4
r. p.
tr.
r. s.
h. m.
o. e.
B
o. e.
r. p.
r. s.
sp. n.
tr.

Figure 73. Dissection of metamorphosed adult *Notophthalmus viridescens* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

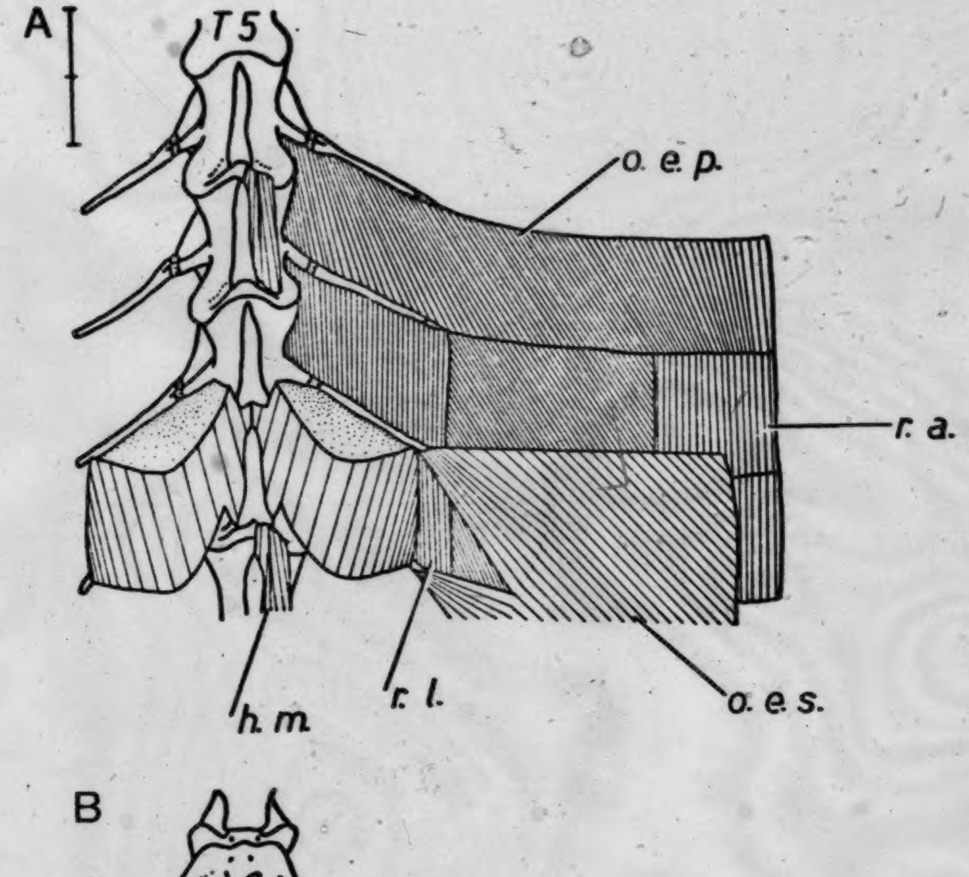

A
T5
o. e. p.
r. a.
h. m.
r. l.
o. e. s.
B
o. e. p.
sp. n.
tr.
o. i.

Figure 74. Dissection of neotenic adult *Notophthalmus viridescens* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, arrows marking ventral edge of *transversus*; scale represents two millimeters; abbreviations given on pp. 4-7.

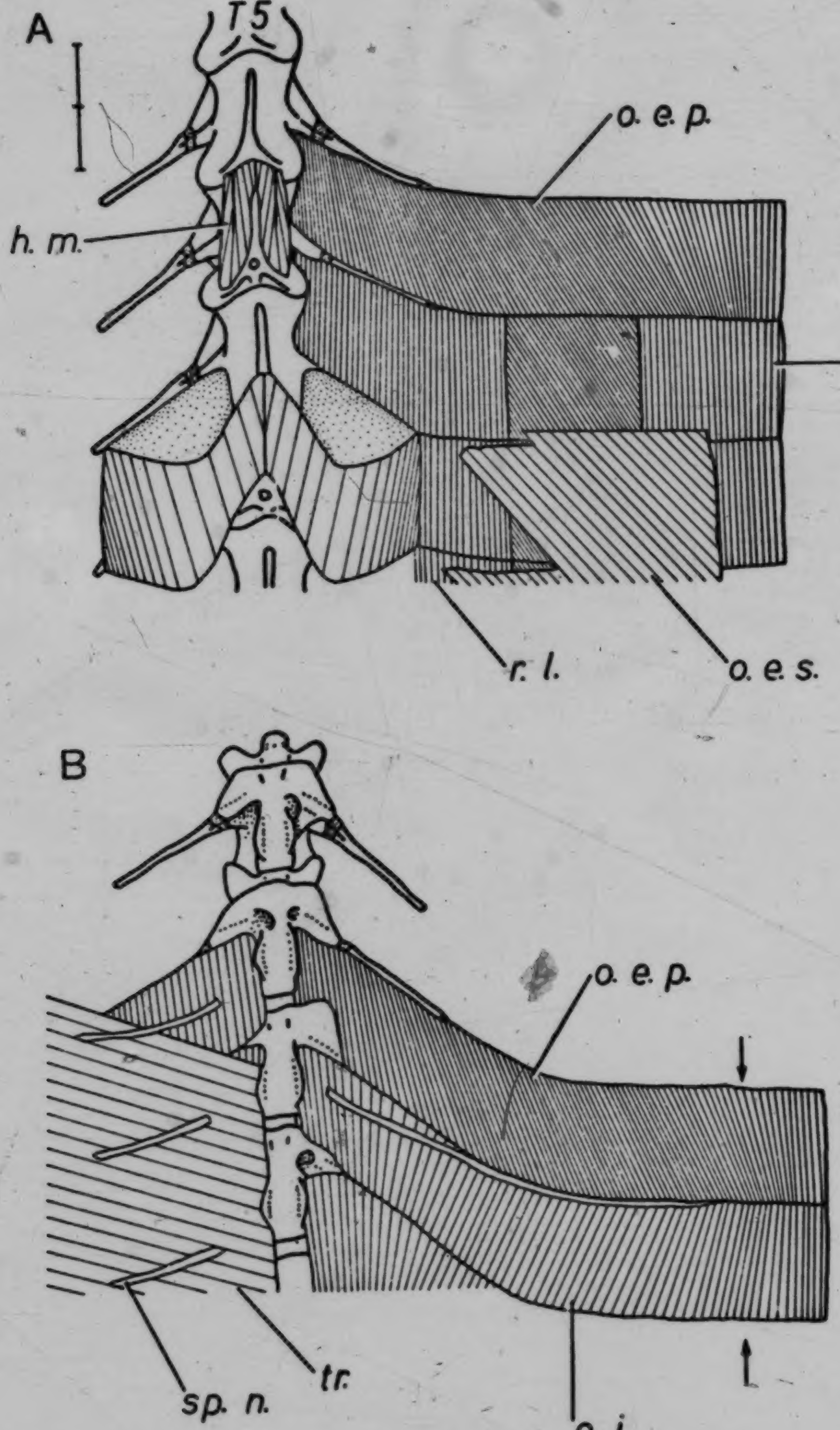
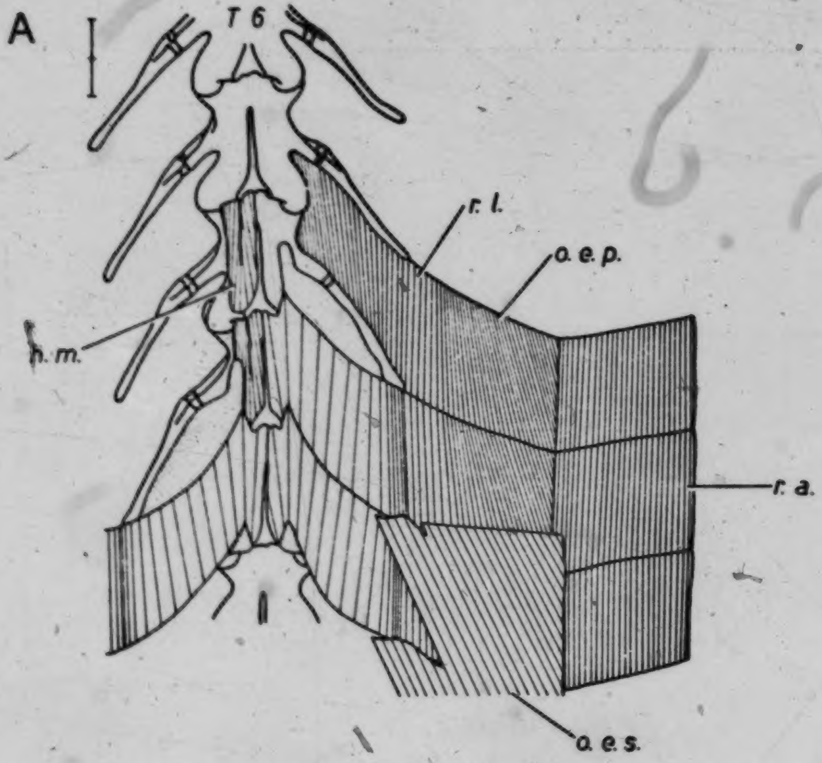

A
T5
o. e. p.
h. m.
r. a.
r. l.
o. e. s.
B
o. e. p.
sp. n.
tr.
o. i.

Figure 75. Dissection of *Taricha* species with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, arrows and dotted line marking edge of *rectus abdominus*, which is not reflected in the direction of the muscle fibers, but is evident in anatomical specimens; scale represents two millimeters; abbreviations given on pp. 4-7.


A
T 6
r. l.
o. e. p.
h. m.
r. a.
o. e. s.

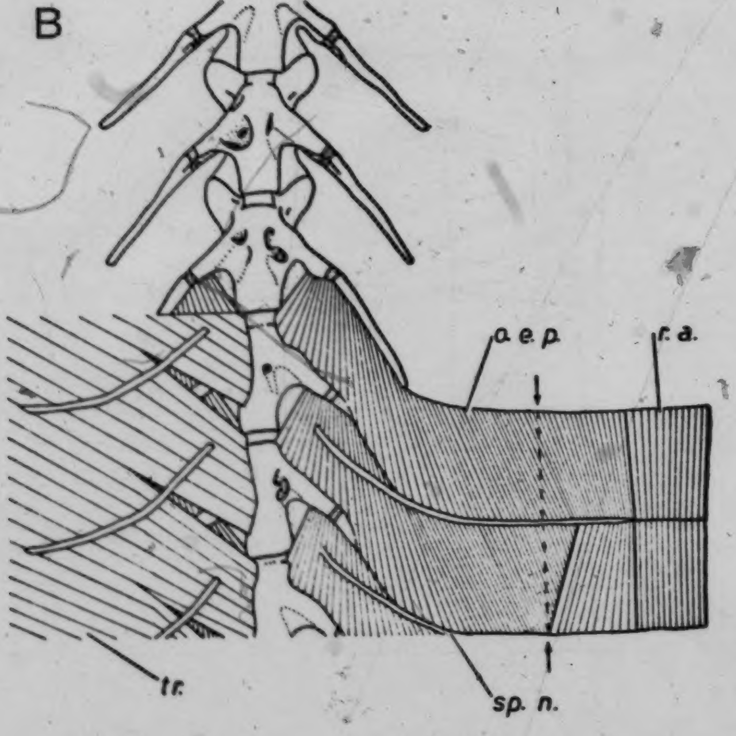

B
o. e. p.
r. a.
tr.
sp. n.

Figure 76. Dissection of *Cynops pyrrhogaster* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

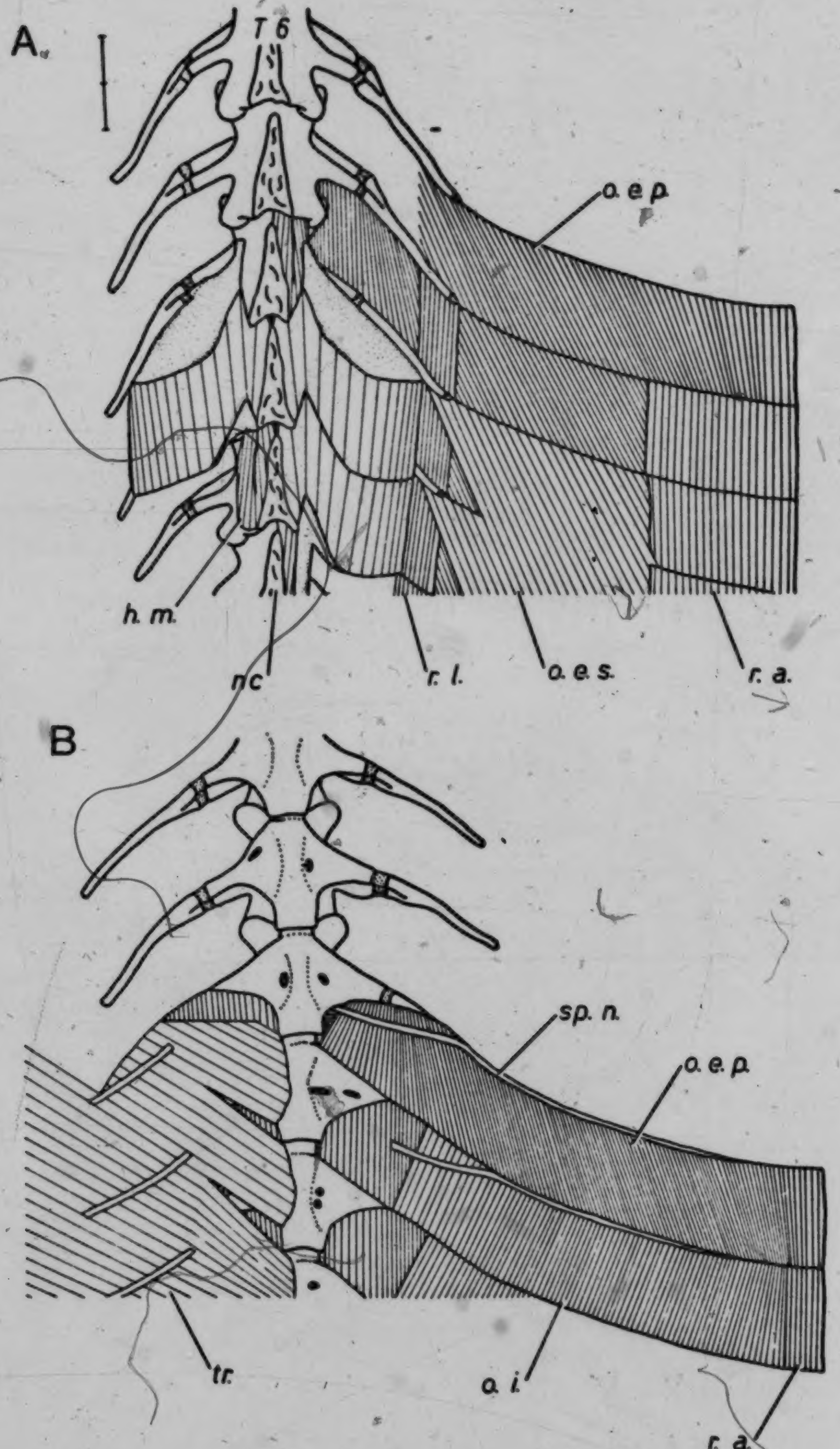

A
T6
o.e.p.
h.m.
nc
r.l.
o.e.s.
r.a.
B
sp.n.
o.e.p.
tr.
o.i.
r.a.

Figure 77. Dissection of *Paramesotriton hongkongense* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

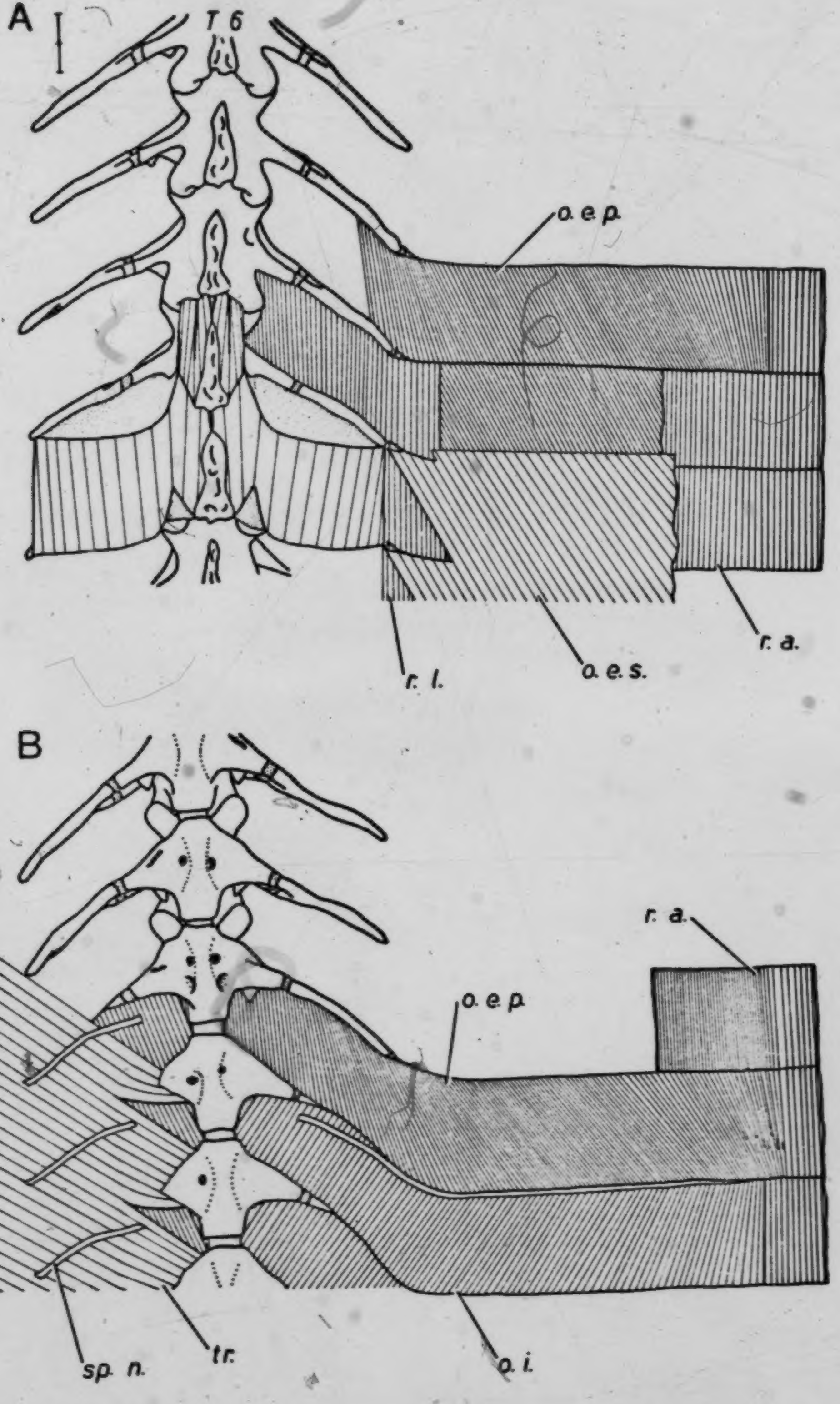

A
T 6
o. e. p.
r. l.
o. e. s.
r. a.
B
r. a.
o. e. p.
sp. n.
tr.
o. i.

Figure 78. Dissection of *Triturus cristatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

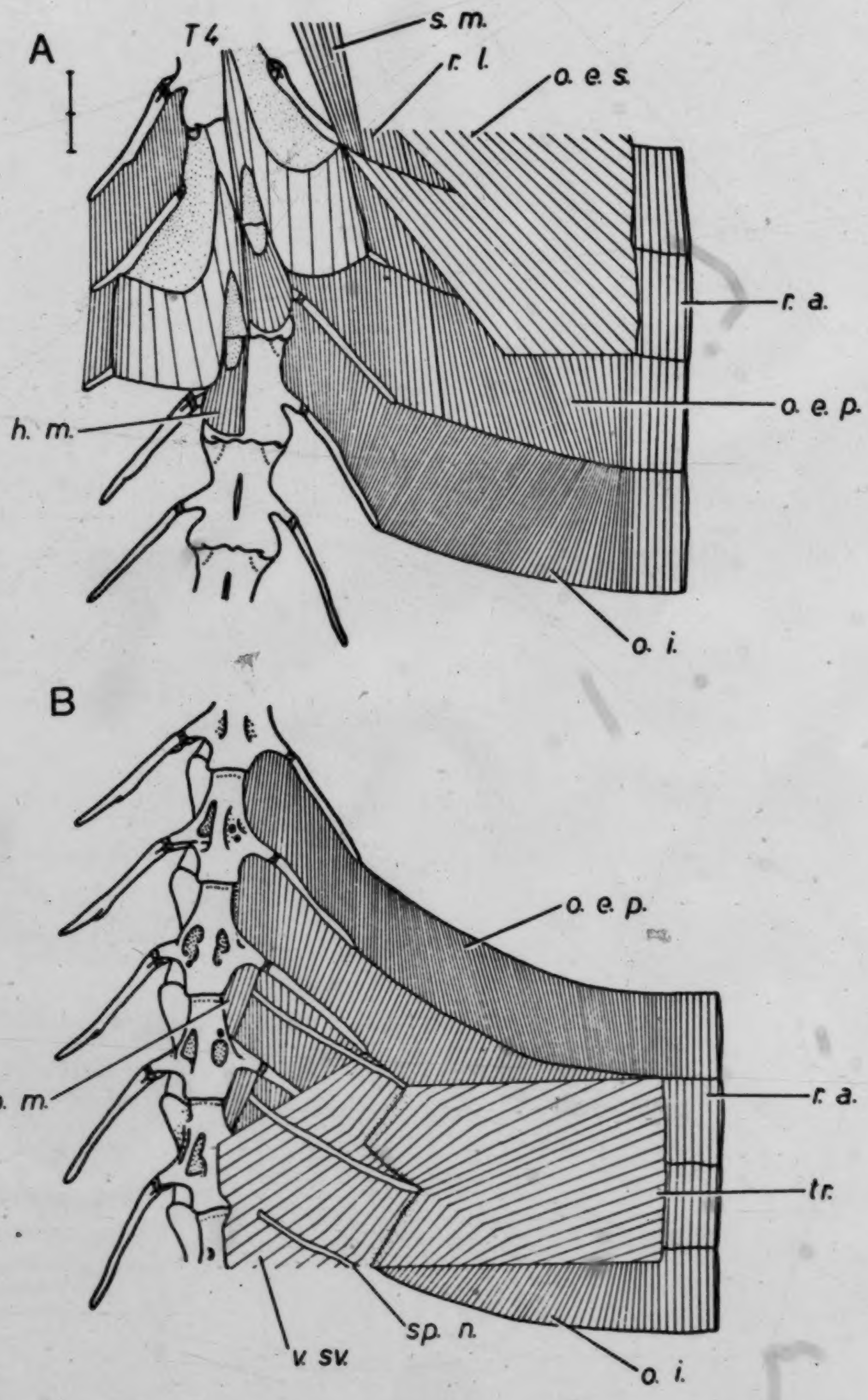

A
T4
s. m.
r. l.
o. e. s.
r. a.
o. e. p.
h. m.
o. i.
B
o. e. p.
t. p. m.
r. a.
tr.
sp. n.
v. sv.
o. i.

Figure 79. Dissection of a laterally flexed specimen of *Triturus marmoratus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

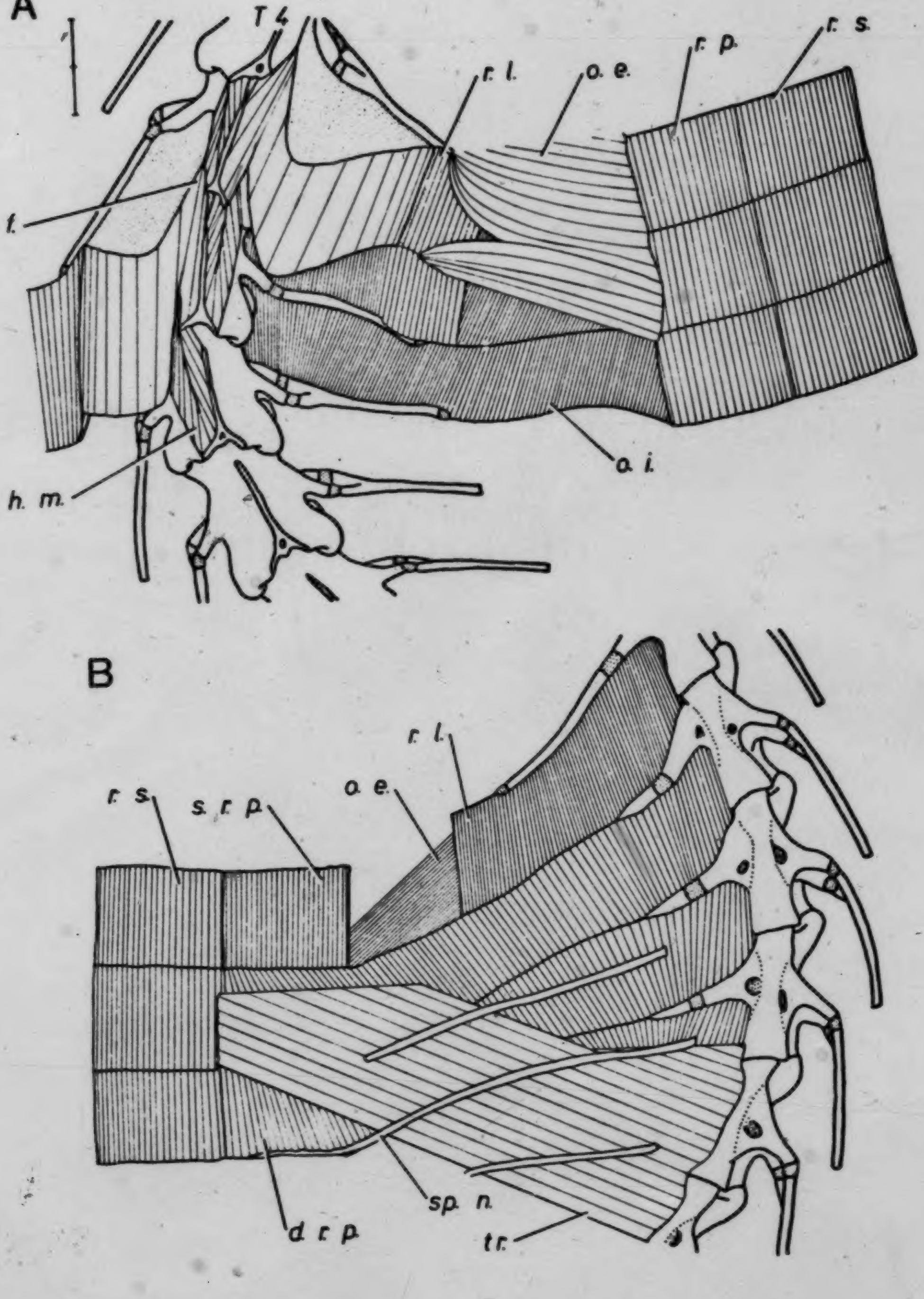

A
T 4
r. l.
o. e.
r. p.
r. s.
a. f.
h. m.
o. i.
B
r. l.
o. e.
r. s.
s. r. p.
d. r. p.
sp. n.
tr.

Figure 80. Dissection of *Triturus alpestris* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

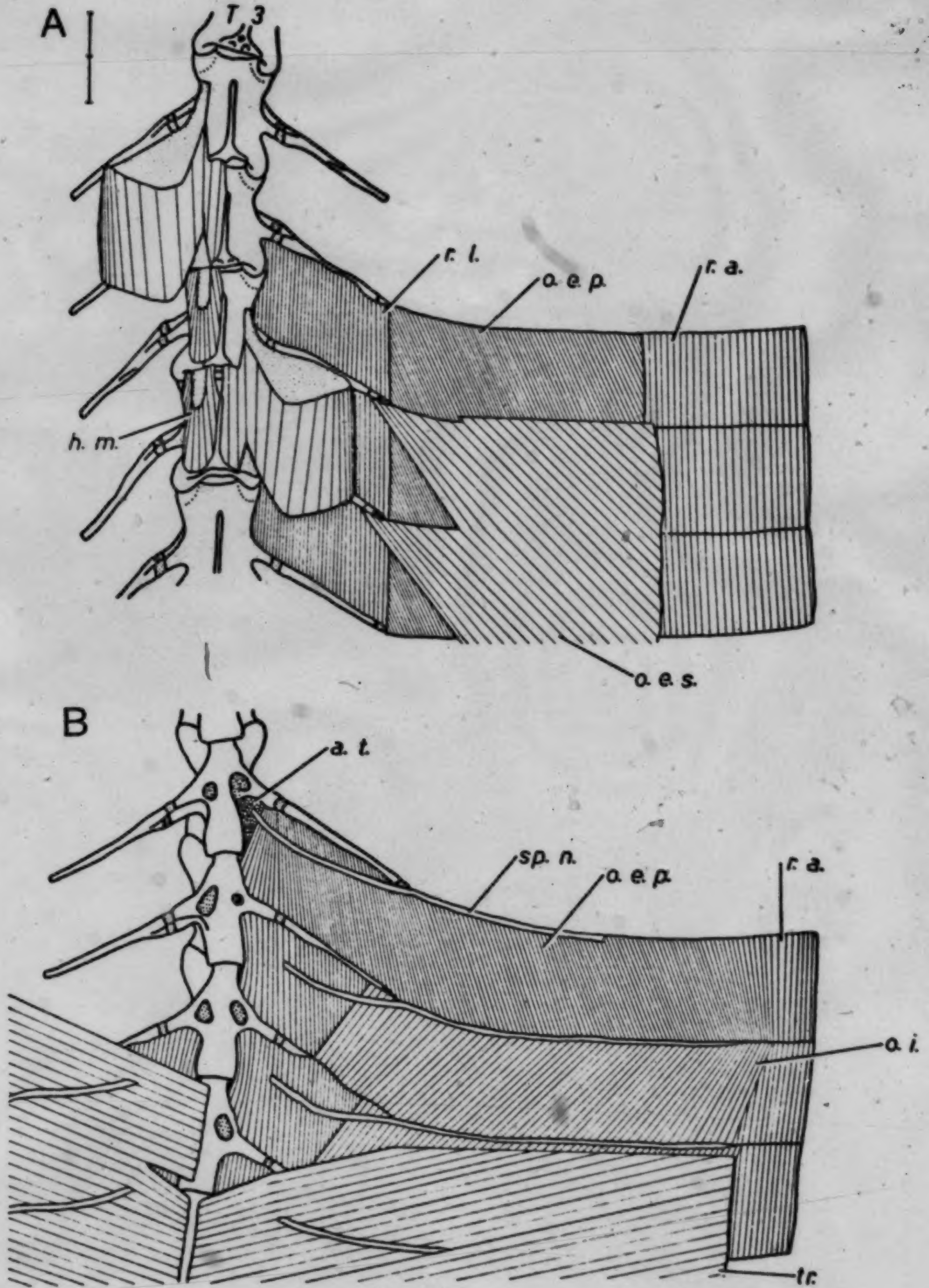

A
T 3
r. l.
o. e. p.
r. a.
h. m.
o. e. s.
B
a. t.
sp. n.
o. e. p.
r. a.
o. i.
tr.

Figure 81. Dissection of *Triturus vittatus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view, arrow and dotted line showing questionable division into *rectus abdominus superficialis* and *rectus abdominus profundus*; scale represents two millimeters; abbreviations given on pp. 4-7.

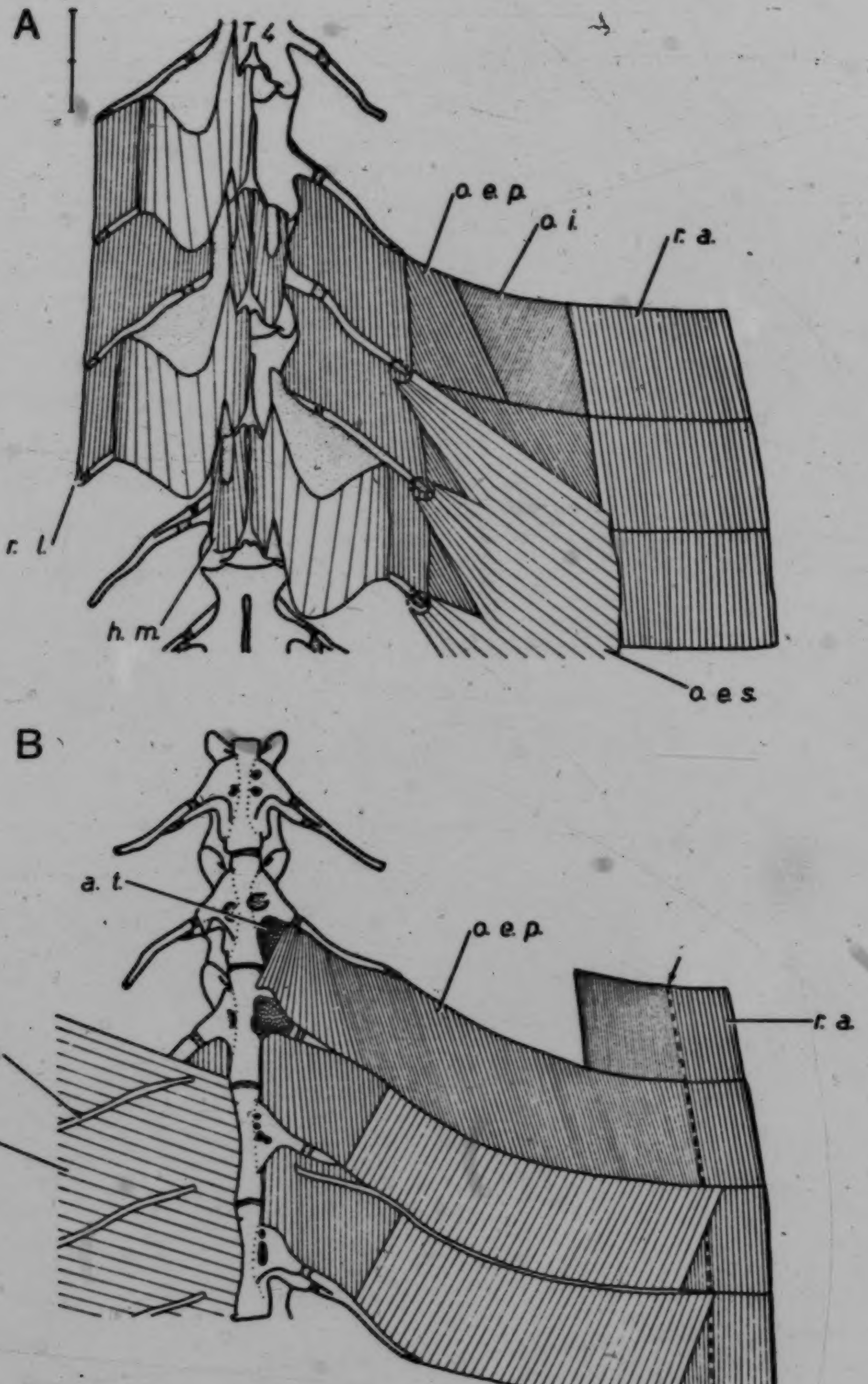

A
T.4
a.e.p.
a.i.
r.a.
r.l.
h.m.
a.e.s.
B
a.t.
a.e.p.
r.a.
sp.n.
tr.
a.i.

Figure 82. Dissection of *Triturus vulgaris* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

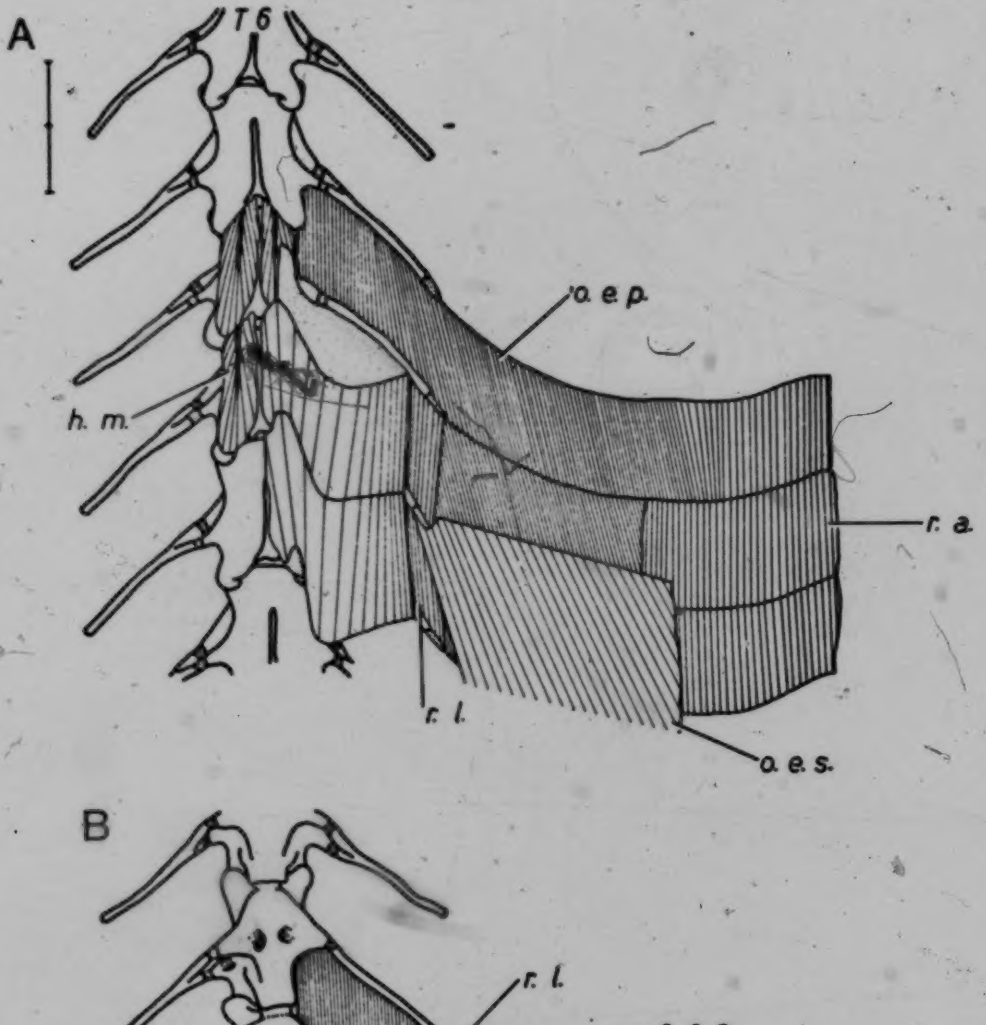
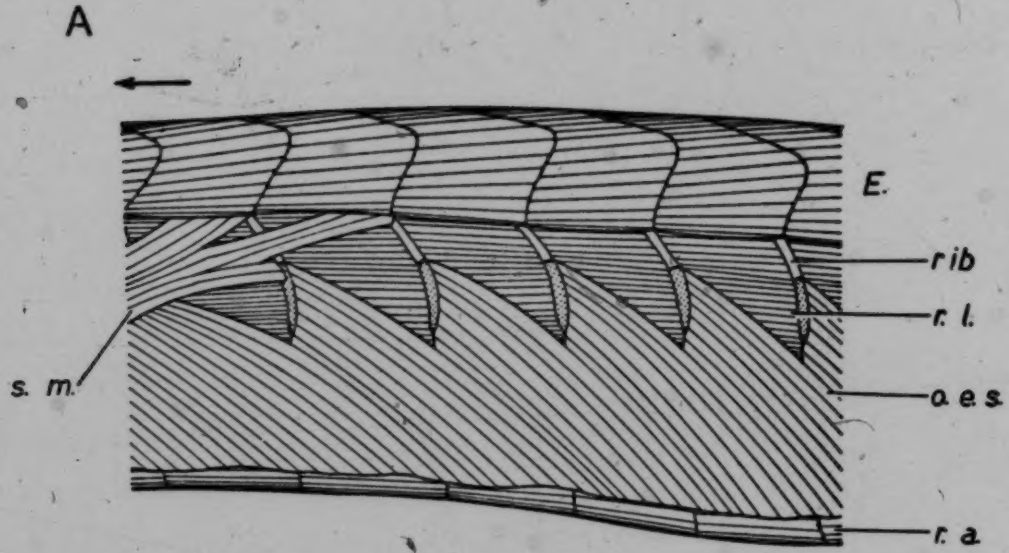

A
T6
o. e. p.
h. m.
r. a.
r. l.
o. e. s.
B
r. l.
o. e. p.
o. i.
sp. n.
tr.
r. a.

Figure 83. Camera lucida sketches of the anterior portion of the trunk of *Triturus vulgaris* just posterior of the pectoral girdle: (A) lateral view, arrow points anteriorly; (B) dorsal view, arrow points anteriorly; abbreviations given on pp. 4-7.


A
E.
rib
r. l.
s. m.
a. e. s.
r. a.

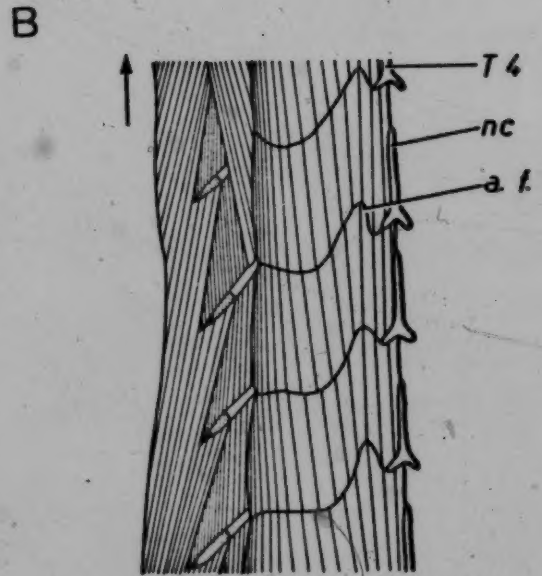

B
T 4
nc
a. f.

Figure 84. Dissection of *Triturus helveticus* with lateral abdominal musculature spread laterally: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

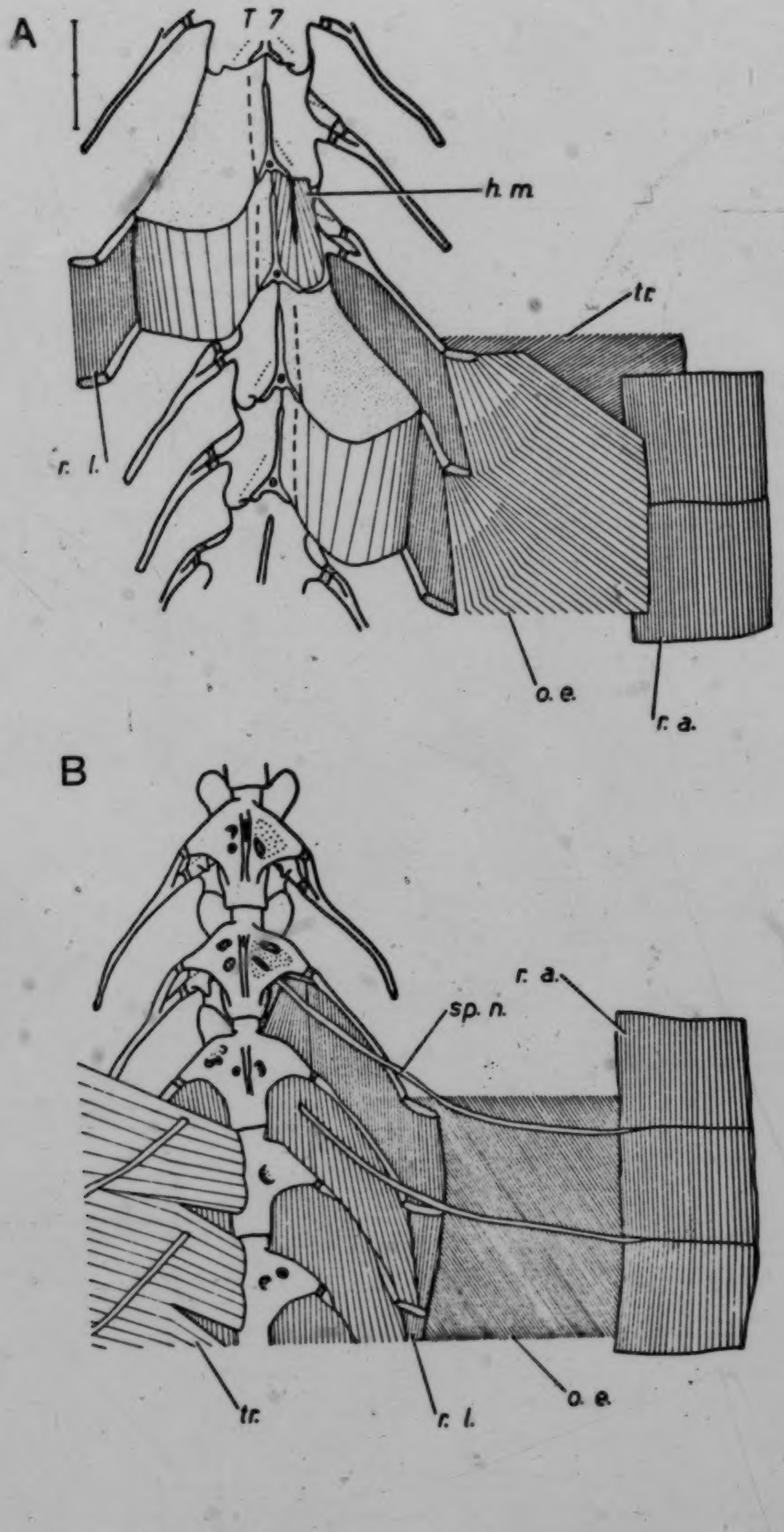

A
T 7
h. m.
tr.
r. l.
o. e.
r. a.
B
r. a.
sp. n.
tr.
r. l.
o. e.

Figure 85. Dissection of *Euproctus asper* with lateral abdominal musculature largely omitted: (A) dorsal view; (B) ventral view; scale represents two millimeters; abbreviations given on pp. 4-7.

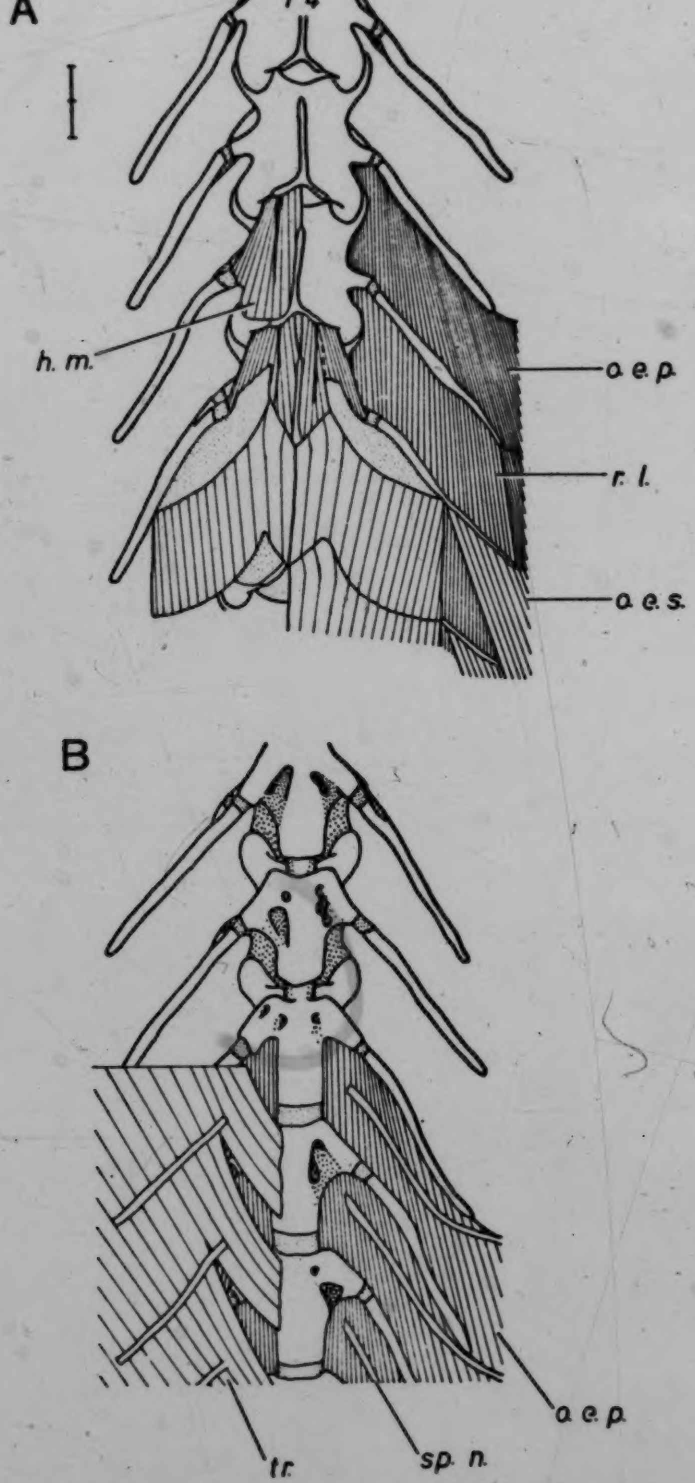
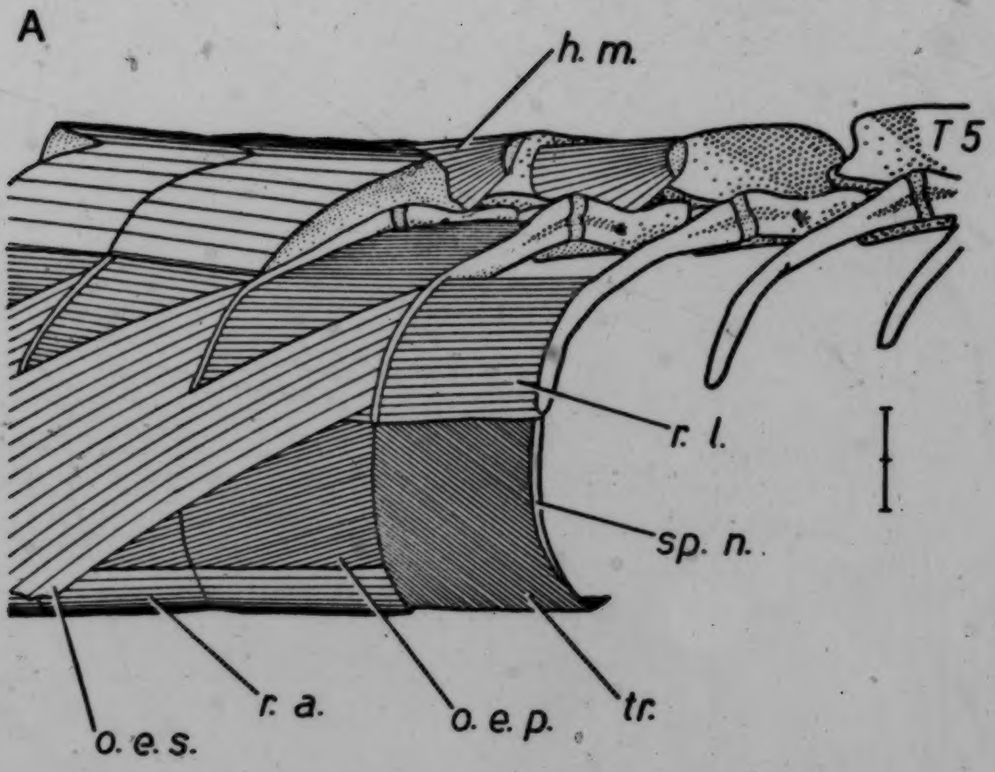

A
T4
h. m.
a. e. p.
r. l.
a. e. s.
B
a. e. p.
tr.
sp. n.

Figure 86. (A) lateral view of trunk of *Euproctus asper*, showing elongate ribs, scale represents two millimeters; (B) vertebrae of *Taricha* species for comparison; abbreviations given on pp. 4-7.


A
h. m.
T 5
r. l.
sp. n.
o. e. s.
r. a.
o. e. p.
tr.

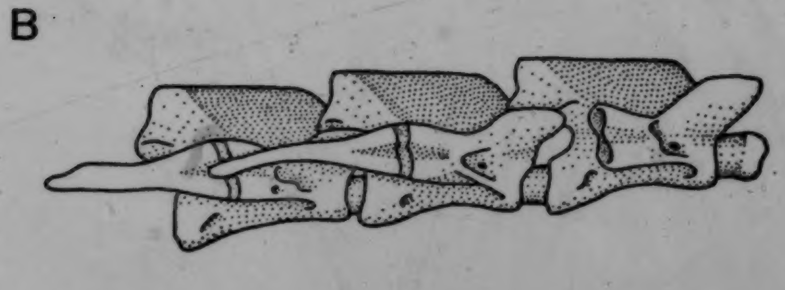

B

Figure 87. Dissection of *Siren lacertina*: (A) dorsal view of deep muscle units of the *dorsalis trunci*; (B) ventral view, lateral abdominal musculature spread laterally; scale represents two millimeters; abbreviations given on pp. 4-7.

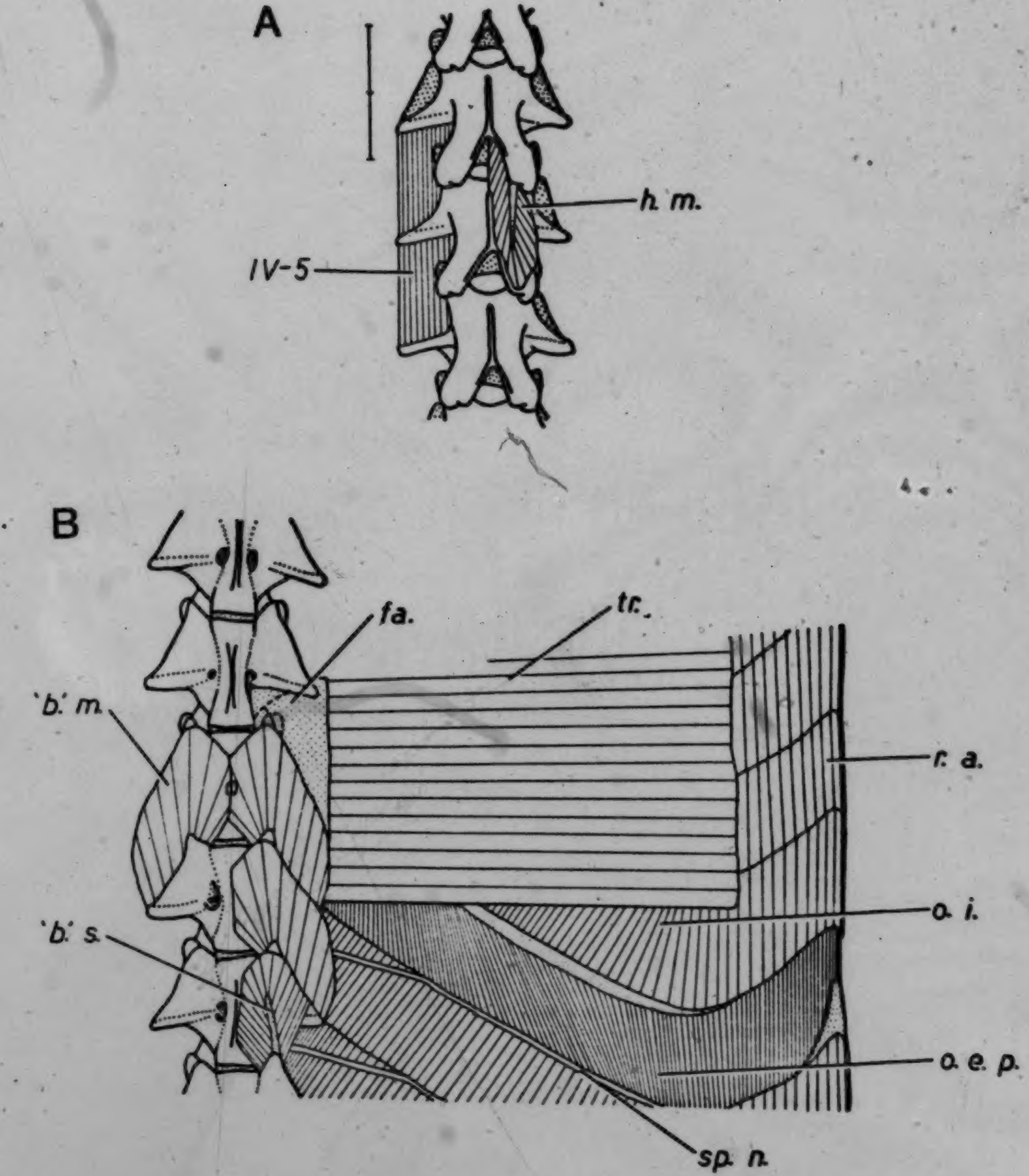

A
h. m.
IV-5
B
fa.
tr.
'b.' m.
r. a.
o. i.
'b.' s.
o. e. p.
sp. n.

Figure 88. Camera lucida sketch of partially dissected trunk of *Siren intermedia* in lateral view, anterior to left; scale represents two millimeters; abbreviations given on pp. 4-7.

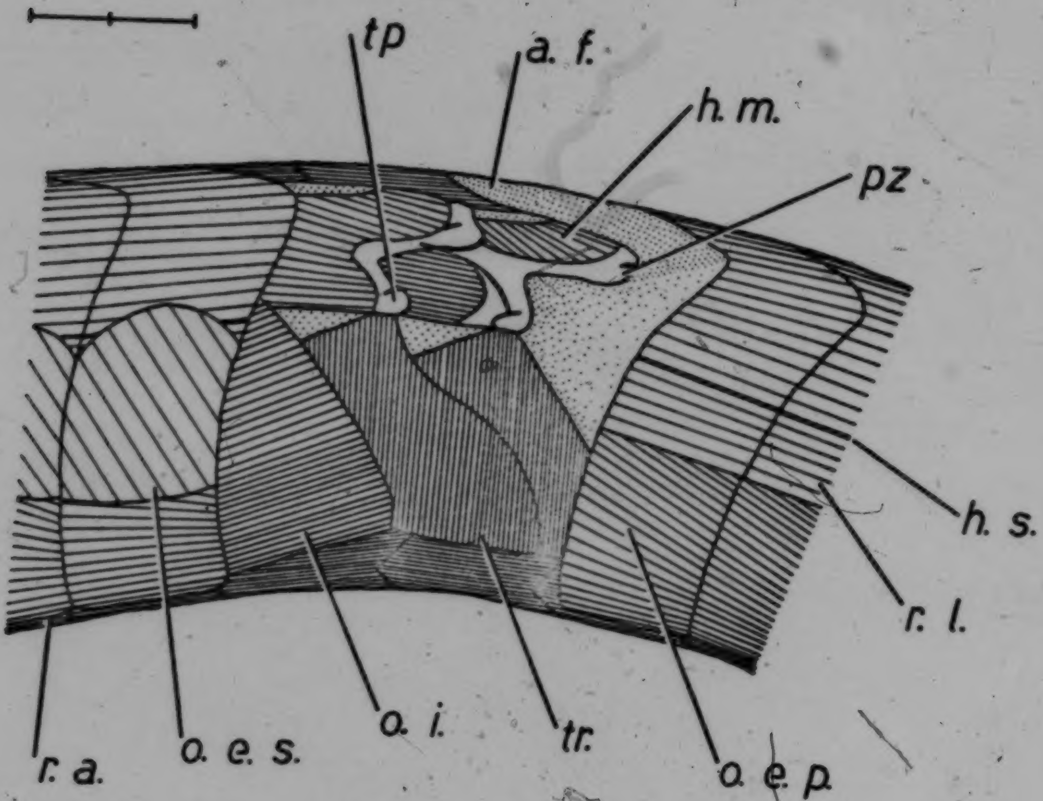

tp
a. f.
h. m.
pz
h. s.
r. l.
r. a.
o. e. s.
o. i.
tr.
o. e. p.

Figure 89. Cross-section through the trunk musculature of large adult *Siren lacertina* drawn with camera lucida; scale represents two millimeters; abbreviations given on pp. 4-7.

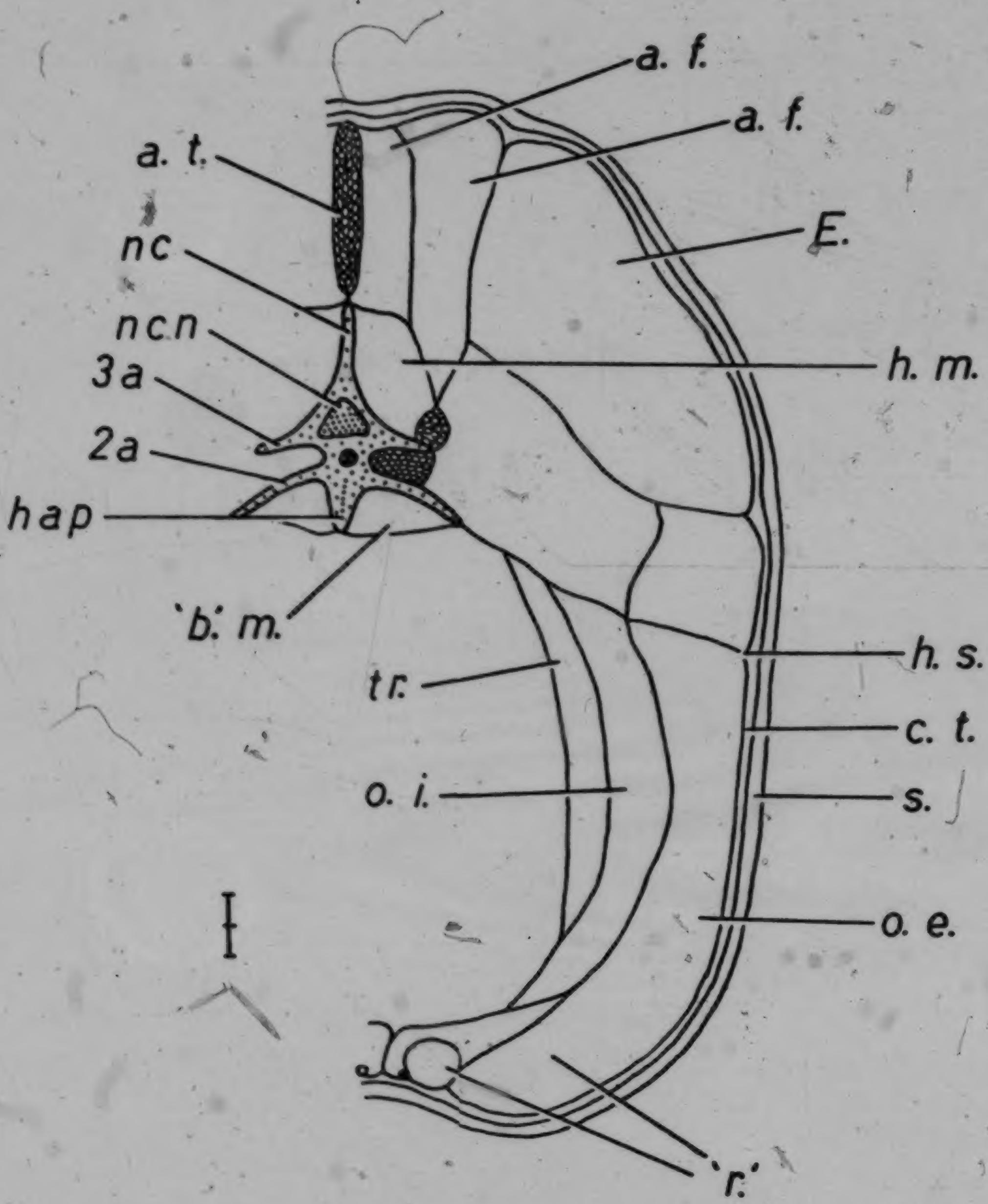

a. f.
a. f.
a. t.
E.
nc
ncn
h. m.
3a
2a
hap
'b.' m.
h. s.
tr.
c. t.
o. i.
s.
o. e.
'r.'

Figure 90. Genera of ambystomatids, plethodontids, and salamandrids forming a morphocline with respect to the *subvertebralis*; see text for discussion.

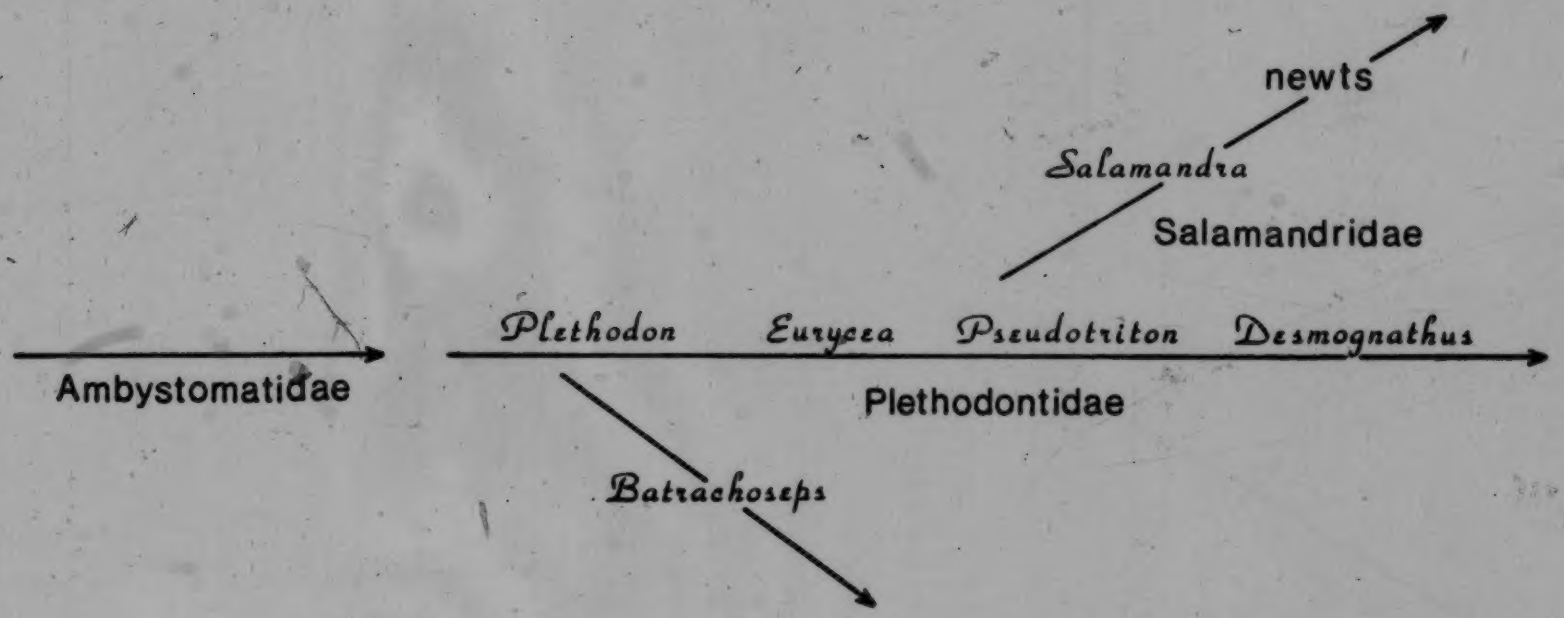
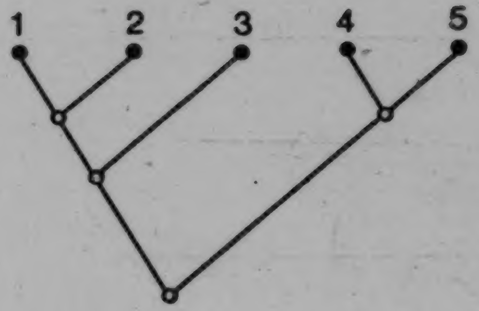
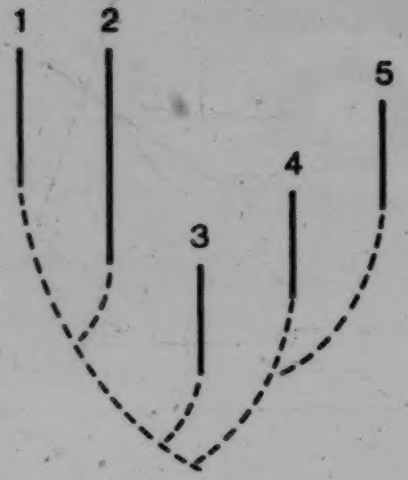

newts
Salamandra
Salamandridae
Ambystomatidae
Plethodon
Eurycea
Pseudotriton
Desmognathus
Plethodontidae
Batrachoseps

Figure 91. Cladistic and evolutionary relationships of a series of hypothetical taxa, after Schaeffer, Hecht, and Eldredge (1972); see text for discussion.





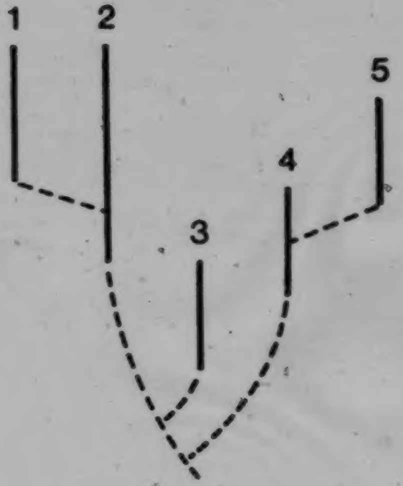


Figure 92. A group of related taxa with the long rectangles indicating shared characters (primitive or derived); see text for discussion.

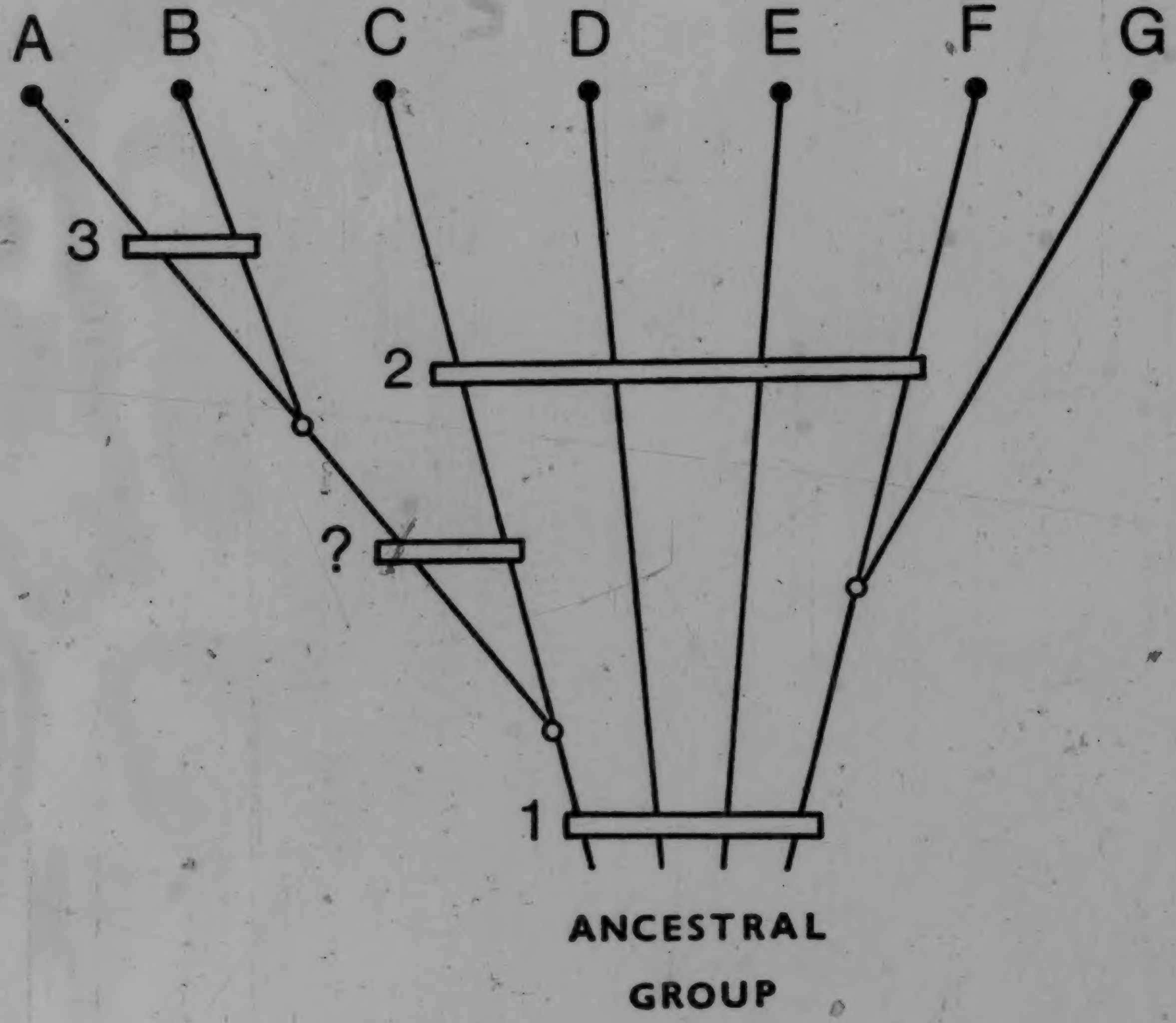

A
B
C
D
E
F
G
3
2
?
1
ANCESTRAL
GROUP

Figure 93. Diagrammatic longitudinal sections across intercentral joints in salamanders, horizontal lines representing notochordal tissue: (A) fully amphicoelous, most primitive; (B) modified amphicoelous with infilling of the cotyles, as in scapherpetontids and amphiumids; (C) opisthocoelous, forming a strengthened joint; (D) opisthocoelous, forming a true ball-and-socket joint.

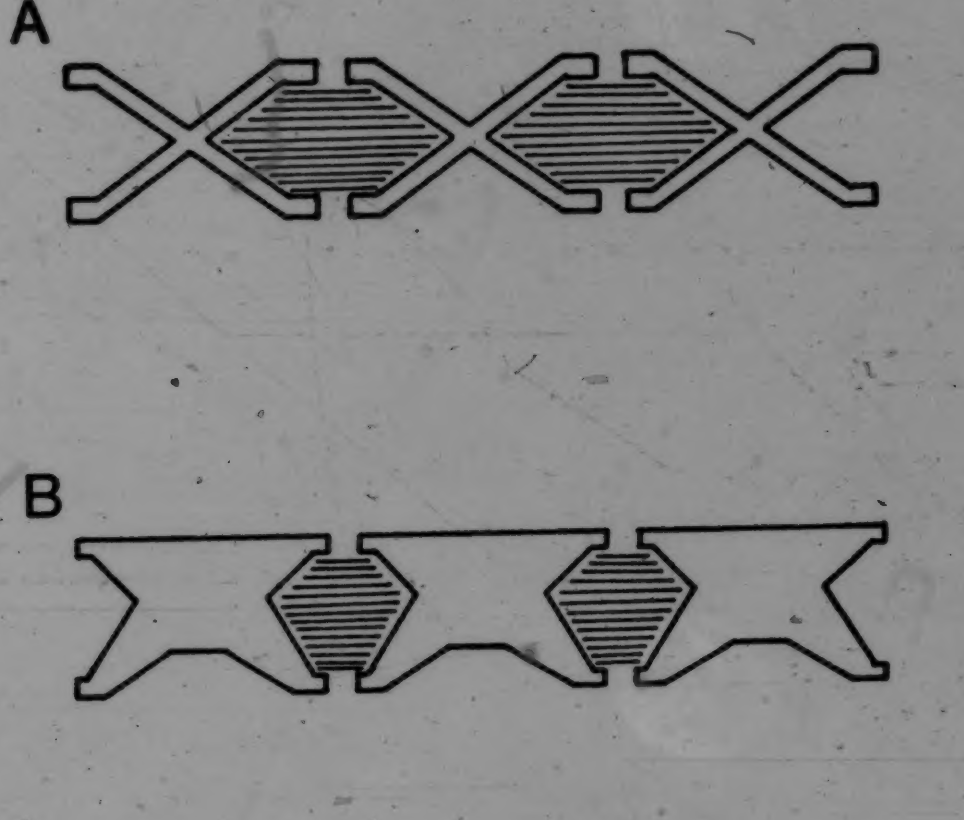

A
B
C
D

Figure 94. Ventral view of midtrunk vertebrae showing different septal patterns of the *subvertebralis*: (A) *Ambystoma jeffersonianum*, basic anterior basapophyseal pattern; (B) *Amphiuma tridactylium*, modified anterior basapophyseal pattern; (C) *Plethodon jordani*, transitional between anterior and posterior basapophyseal patterns: (D) *Plethodon glutinosus*, basic posterior basophyseal pattern; arrows show directions of pull on and between septa.

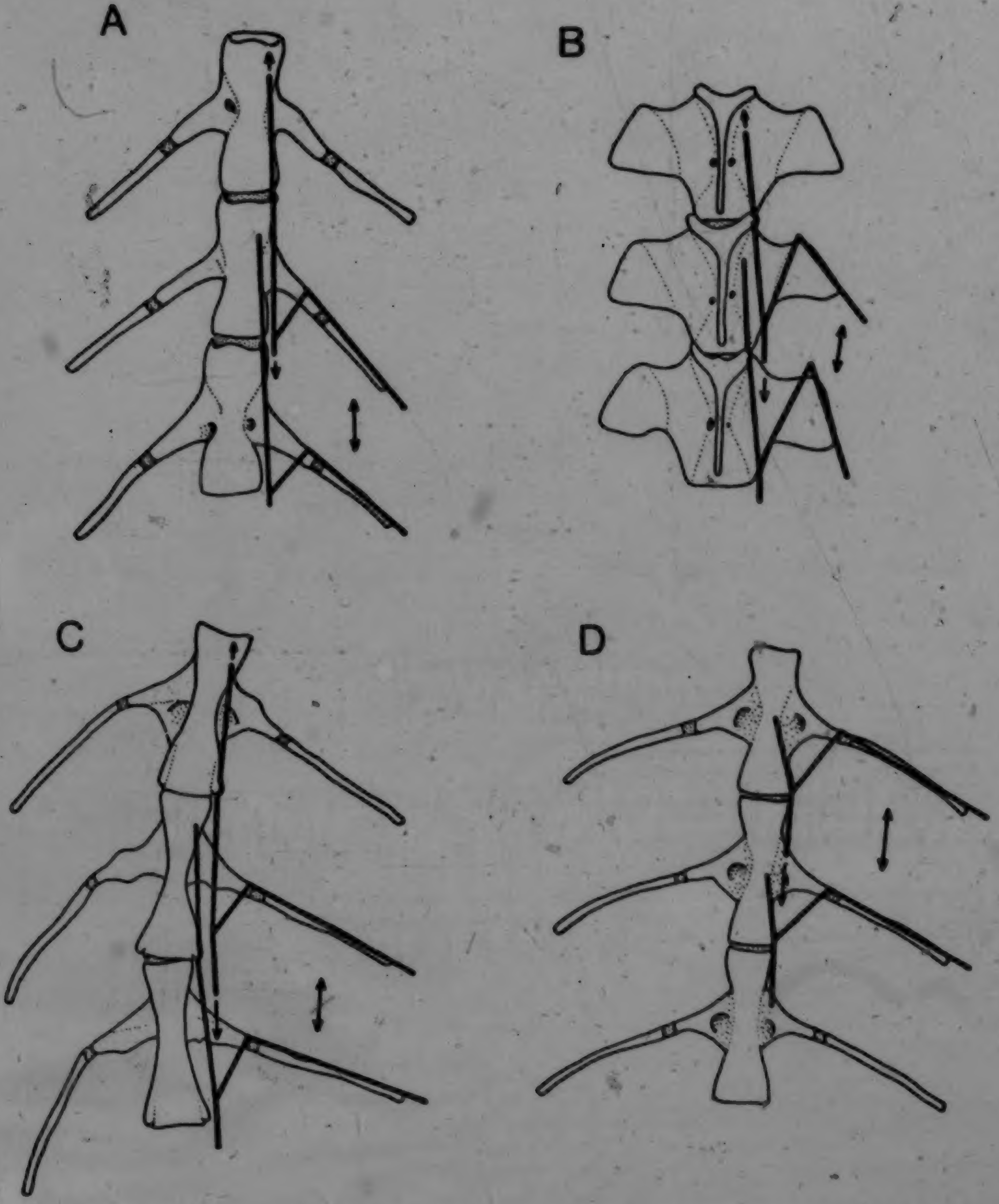

A
B
C
D

Figure 95. Ventral views of midtrunk vertebrae showing septal patterns of the *subvertebralis* in neocaudates: (A) *Gyrinophilus*; (B) *Pseudotriton*; (C) *Desmognathus*, full development of posterior basapophyseal muscle; (D) *Batrachoseps attenuatus*, suppression of subvertebral septa and flexures; arrows show directions of pull on and between septa.

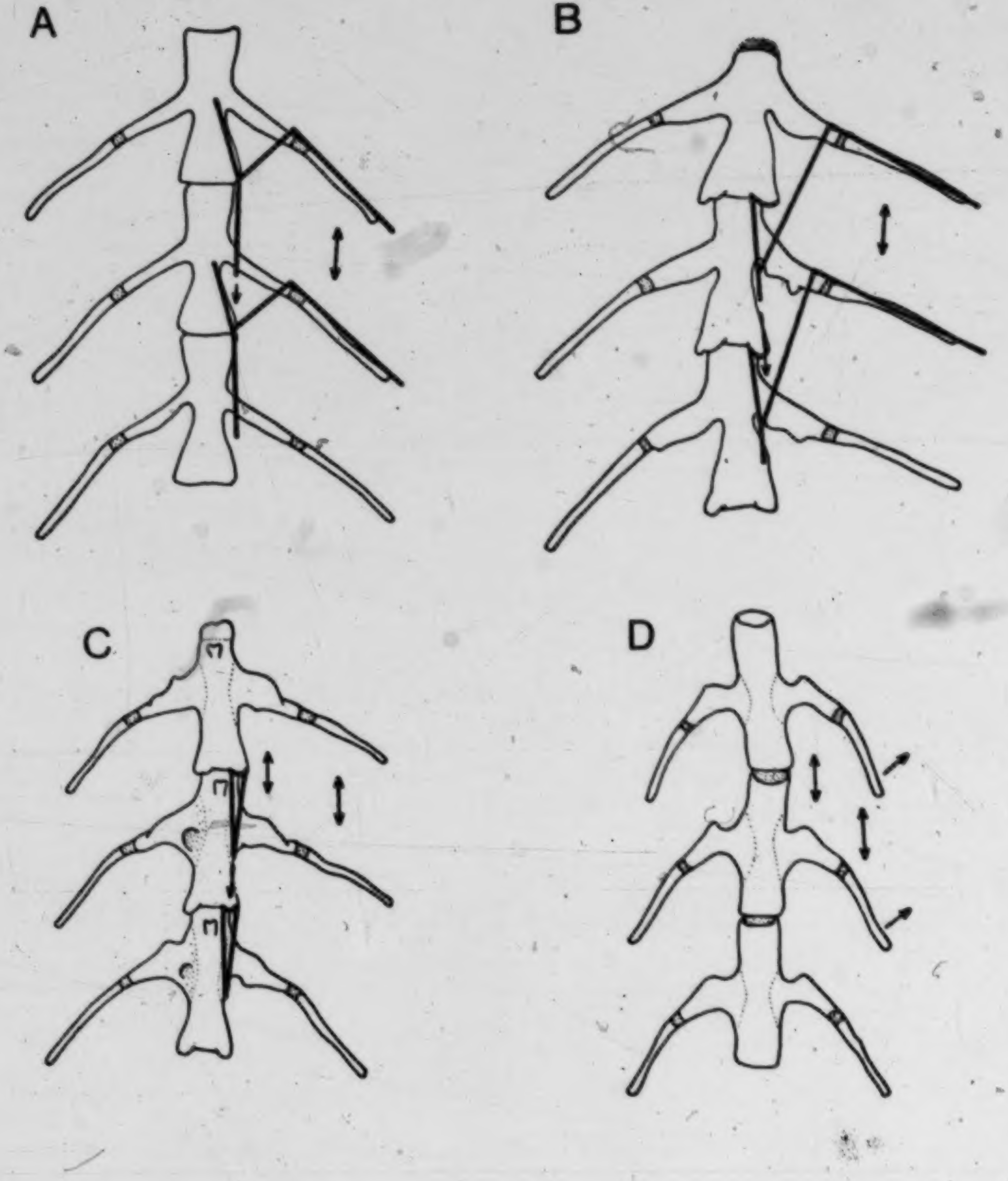

A
B
C
D

Figure 96. Ventral view of midtrunk vertebrae showing septal patterns of the *subvertebralis* in derived Neocaudates: (A) *Salamandra salamandra*l (B) *Necturus maculosus*; arrows show directions of pull on and between septa.

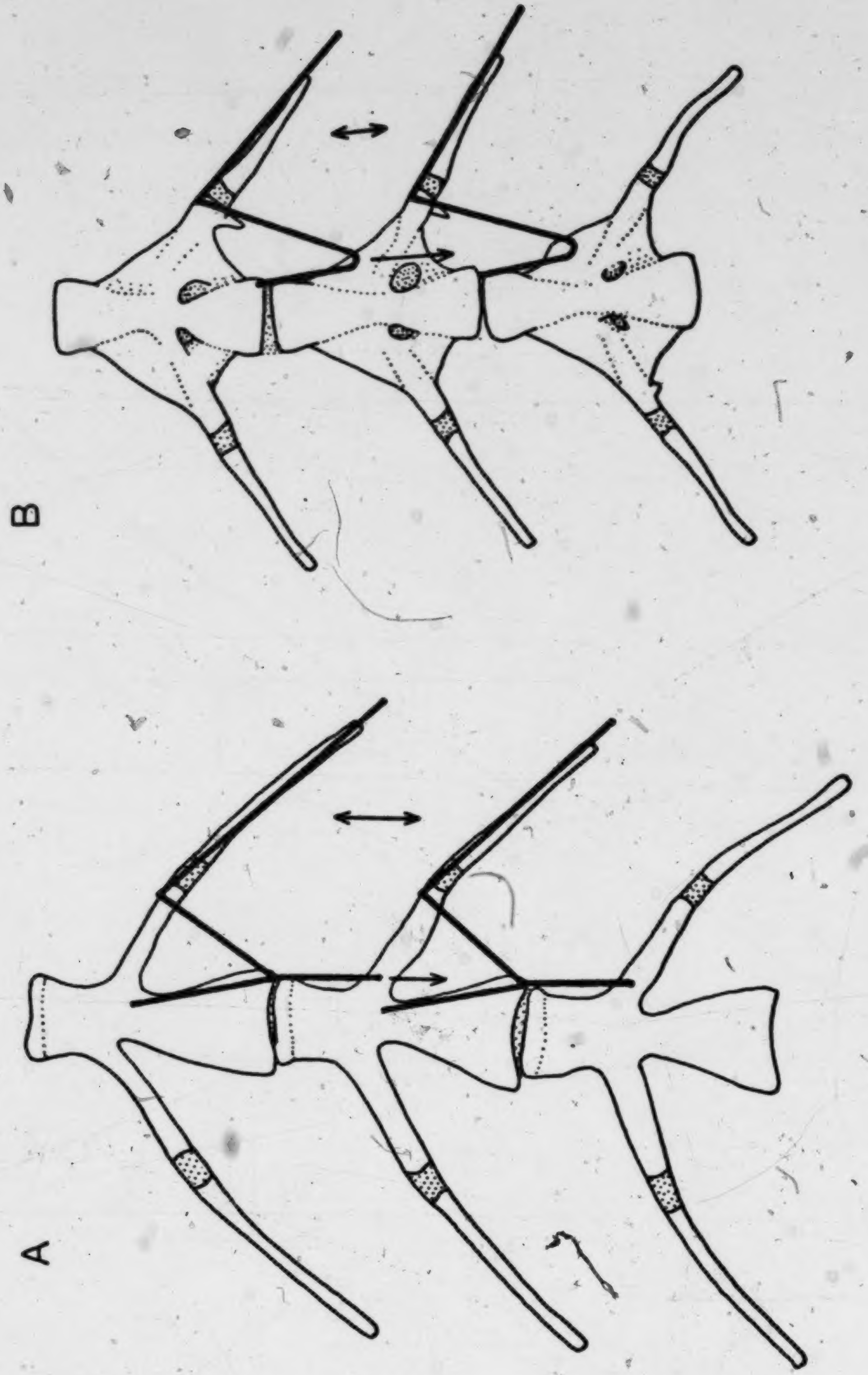

B
A

Figure 97. Ventral views of midtrunk vertebrae showing directions of muscle action in animals that have lost subvertebral flexures: (A) *Triturus helveticus*, showing pattern of the opisthocoelous newts; (B) *Siren*, showing secondary development of a "basapophyseal" muscle, probably from the situation seen in newts; (C) a lizard, showing convergence in a procoelous reptile with the opisthocoelous newts.

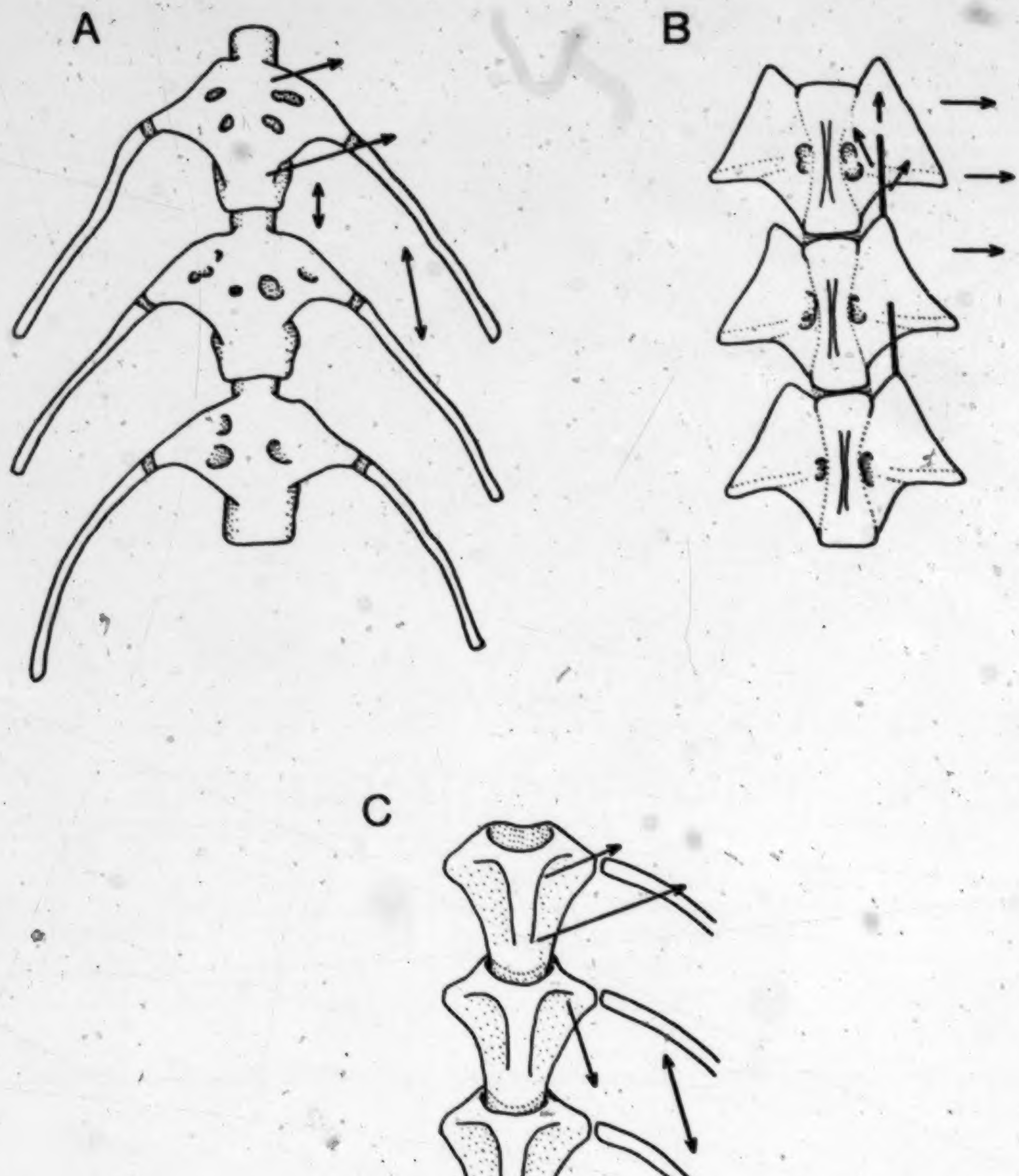
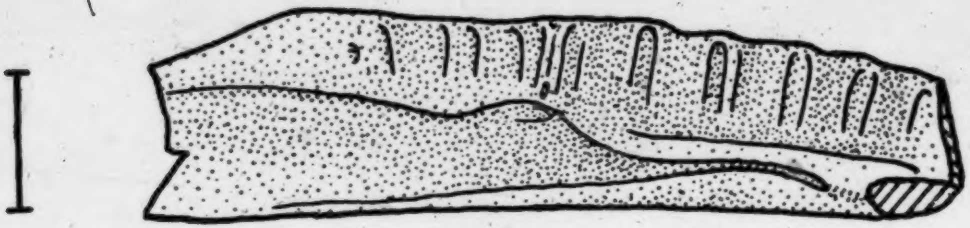
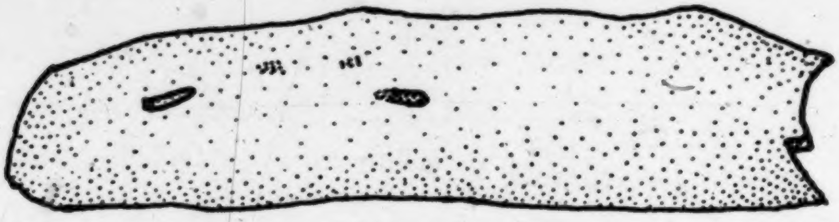

A
B
C

Figure 98. Left dentary (UA 14316) referred to *Proamphiuma cretacea*; from the Bug Creek Anthills locality, Upper Cretaceous Hell Creek Formation, Montana.





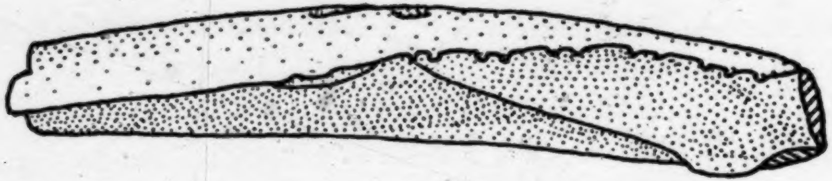


Figure 99. Proposed cladistic relationships within the family Ambystomatidae; species groups differ from those of Tihen (1958), being defined in the text and in Table 1; see text for discussion.

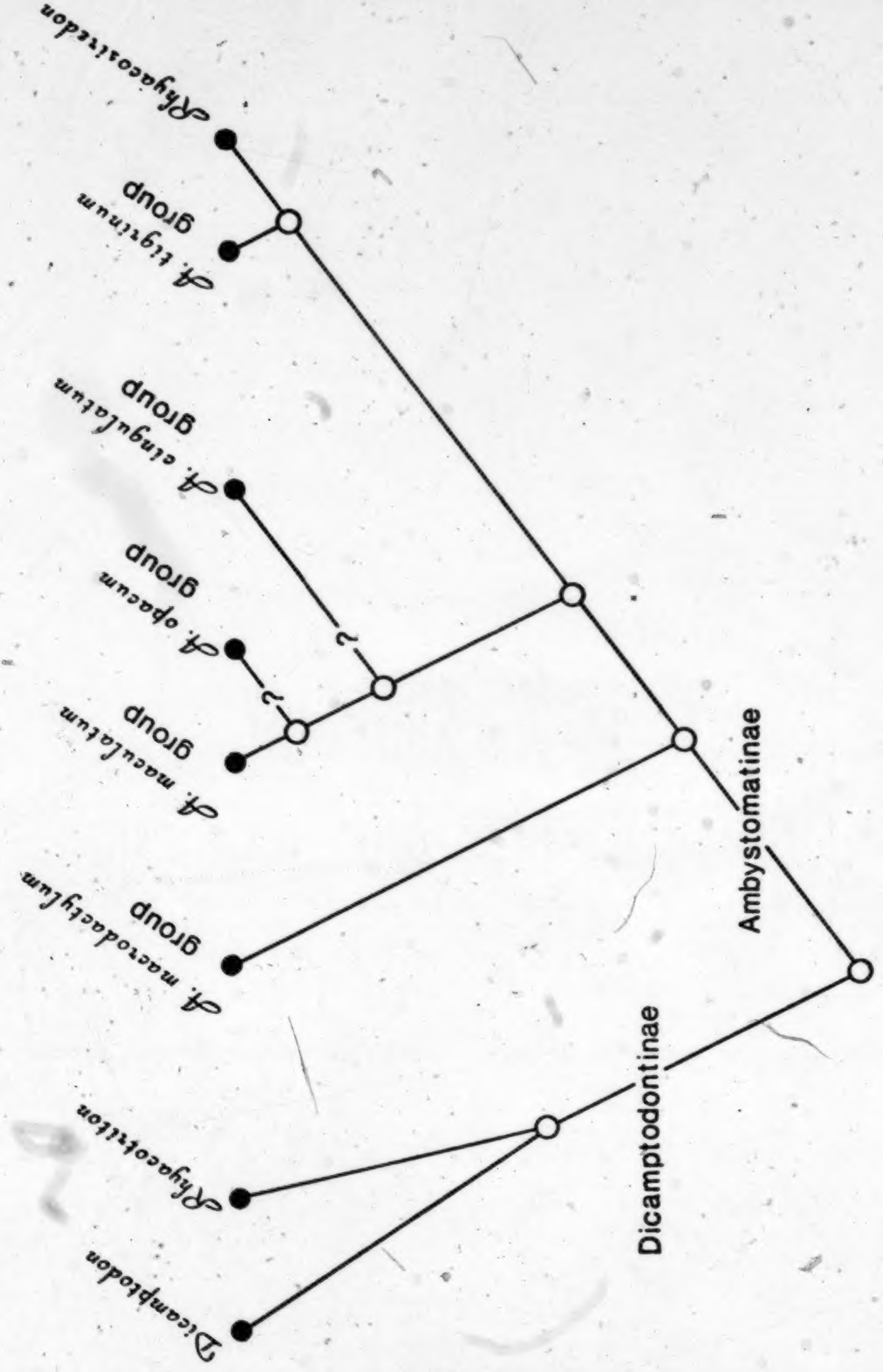

Rhyacosiredon
A. tigrinum group
A. cingulatum group
?
A. opacum group
?
A. maculatum group
A. macrodactylum group
Ambystomatinae
Dicamptodontinae
Rhyacotriton
Dicamptodon

Figure 100. Proposed cladistic relationships within the family Plethodontidae; tribes and subfamilies differ from those of Wake (1966), being defined in the text and in Table 2; see text for discussion.

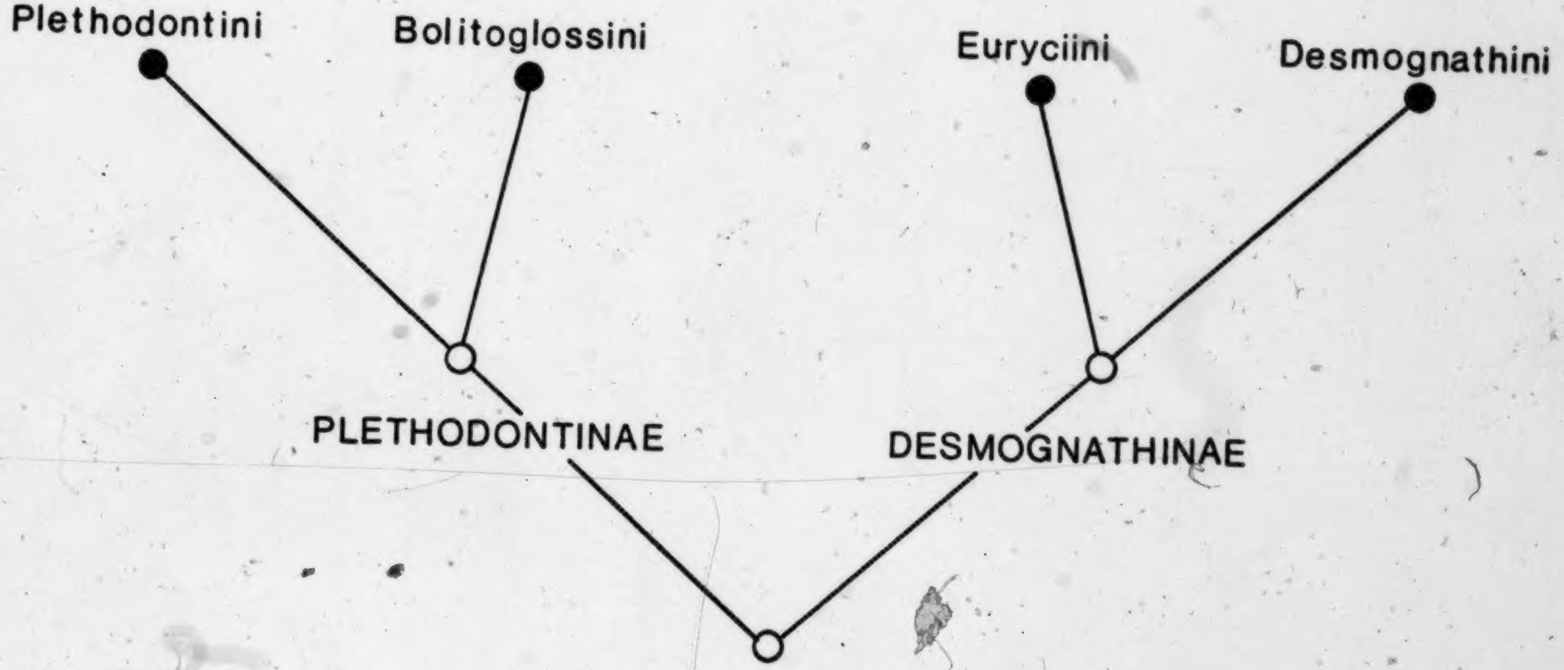

Plethodontini
Bolitoglossini
Euryciini
Desmognathini
PLETHODONTINAE
DESMOGNATHINAE

Figure 101. Proposed cladistic relationships within the family Salamandridae; generic groups are defined in the text and in Table 3; see text for discussion.

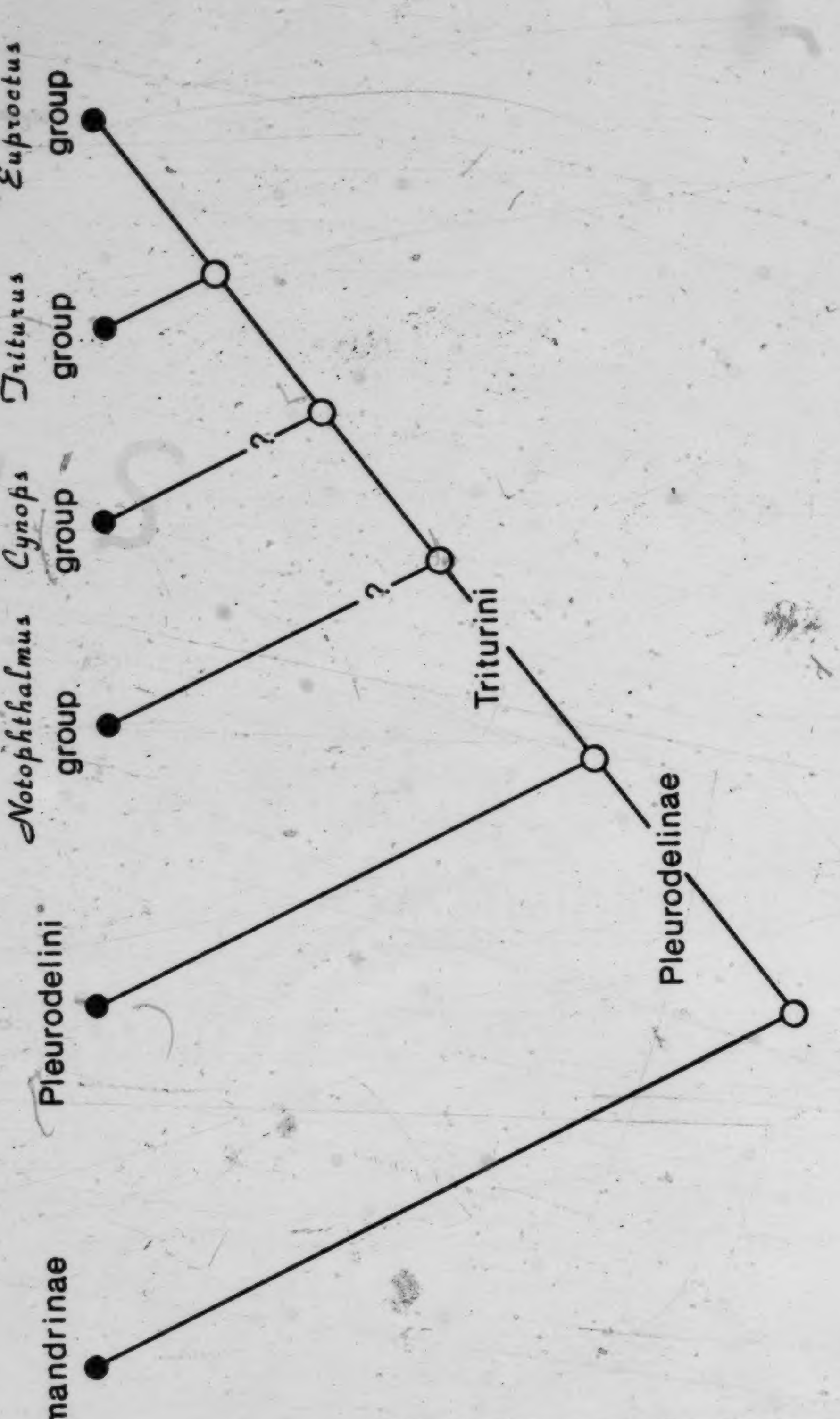

Salamandrinae
Pleurodelini
Notophthalmus group
Cynops group
Triturus group
Euproctus group
?
?
Triturini
Pleurodelinae

Figure 102. Proposed cladistic relationships for the suborder Archaeocaudata; see text for discussion.

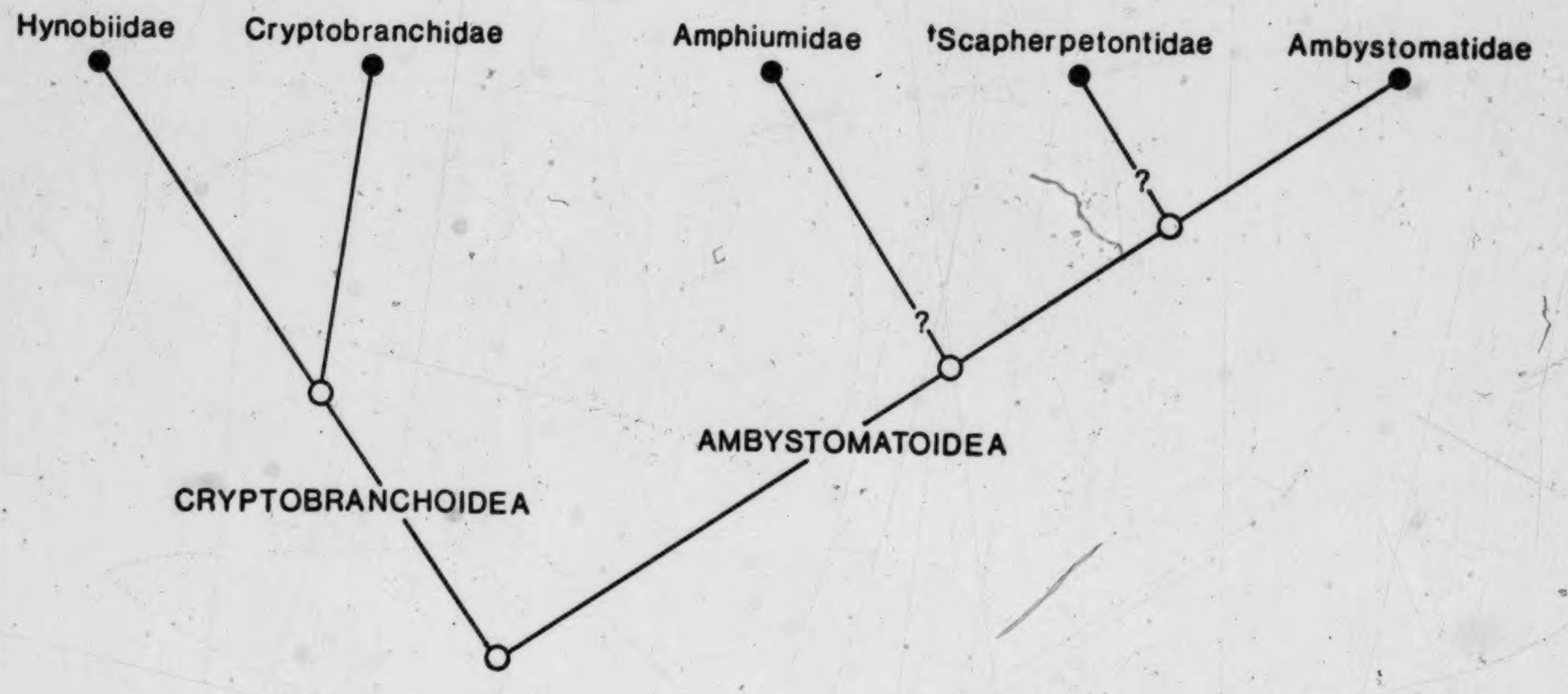

Hynobiidae
Cryptobranchidae
Amphiumidae
†Scapherpetontidae
Ambystomatidae
?
?
AMBYSTOMATOIDEA
CRYPTOBRANCHOIDEA

Figure 103. Proposed cladistic relationships for the suborder Neocaudata; see text for discussion.

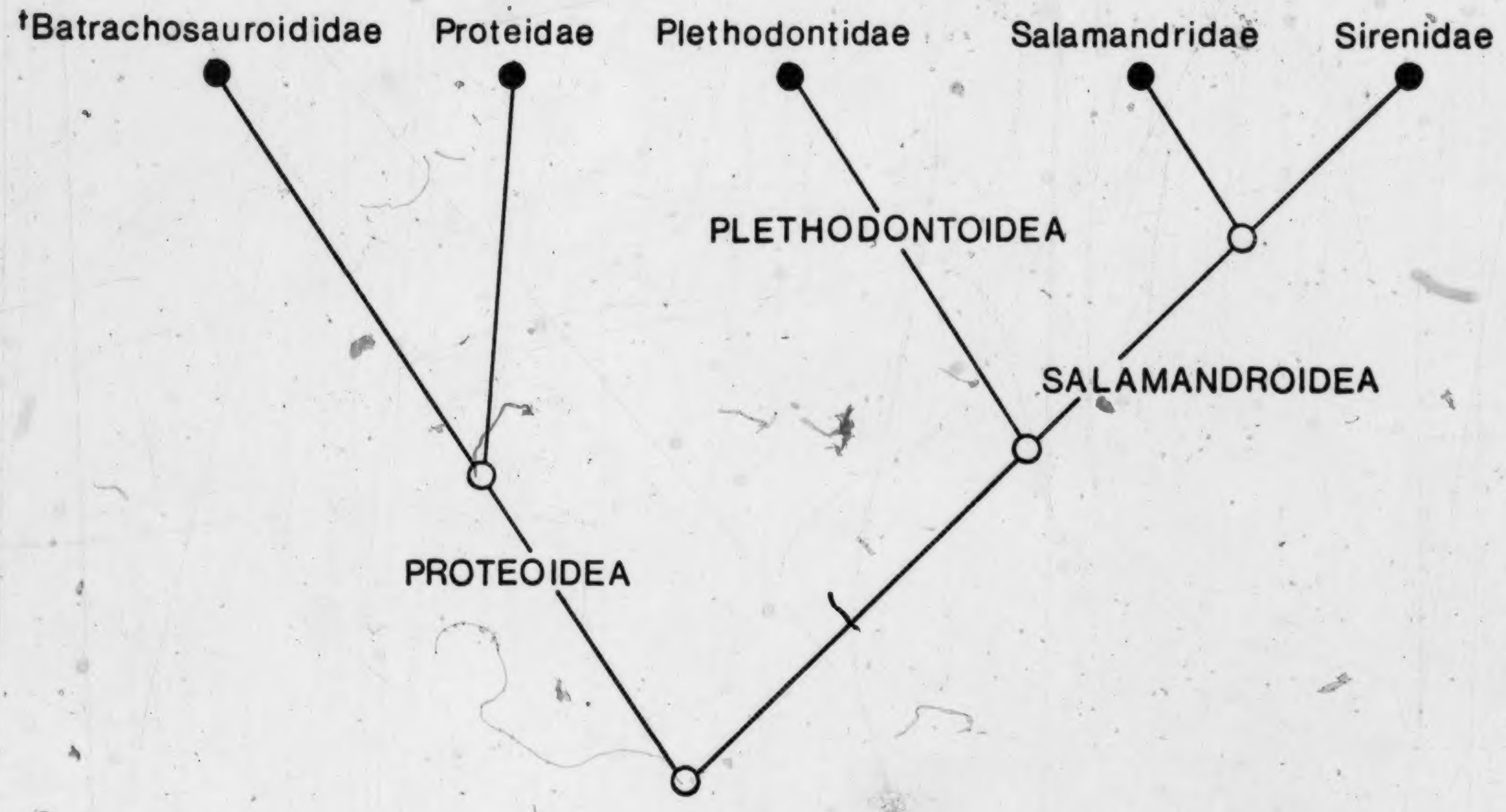

†Batrachosauroididae
Proteidae
Plethodontidae
Salamandridae
Sirenidae
PLETHODONTOIDEA
SALAMANDROIDEA
PROTEOIDEA

Figure 104. Phylogenetic reconstruction proposed for the order Caudata; see text for discussion.

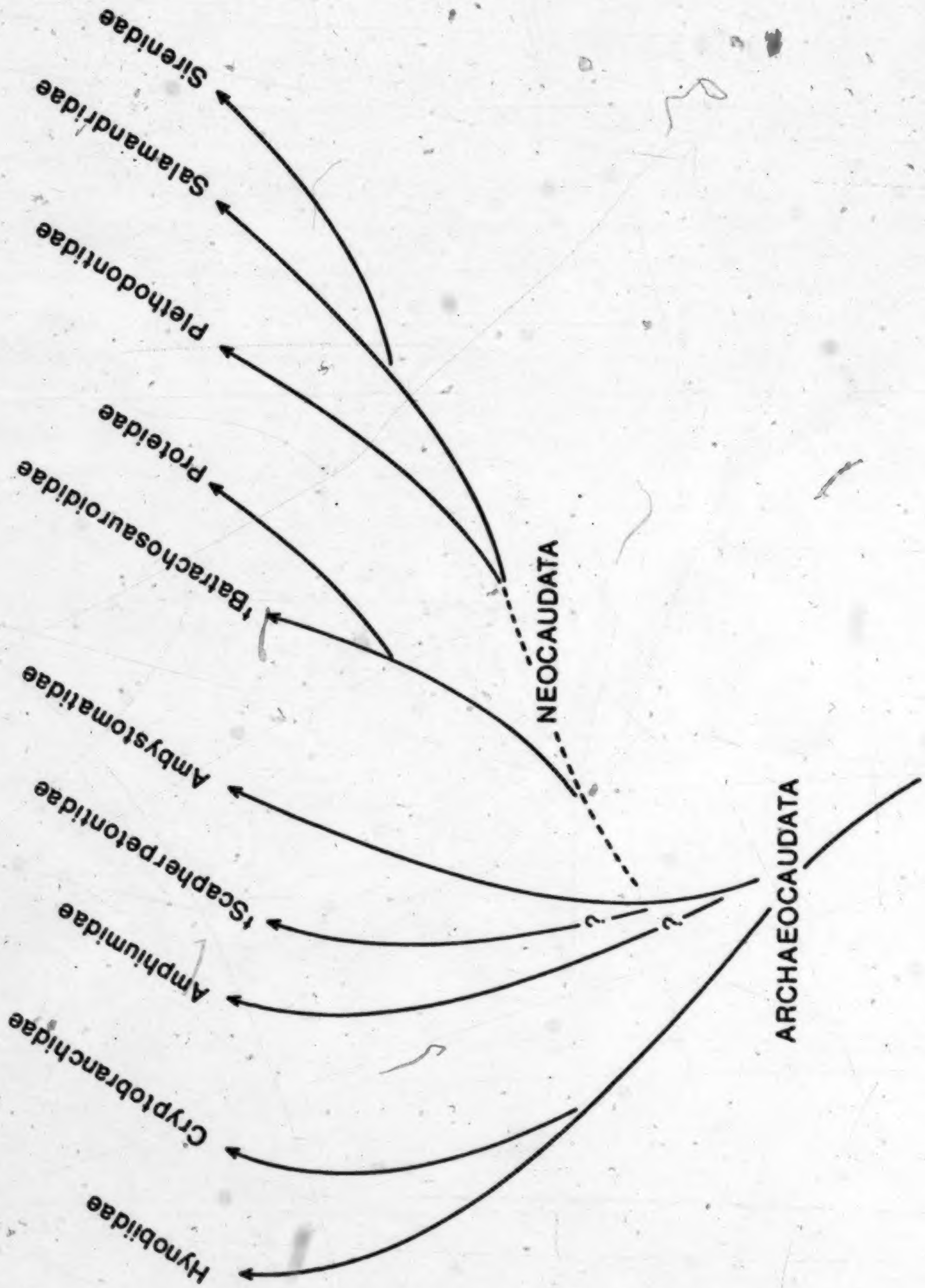
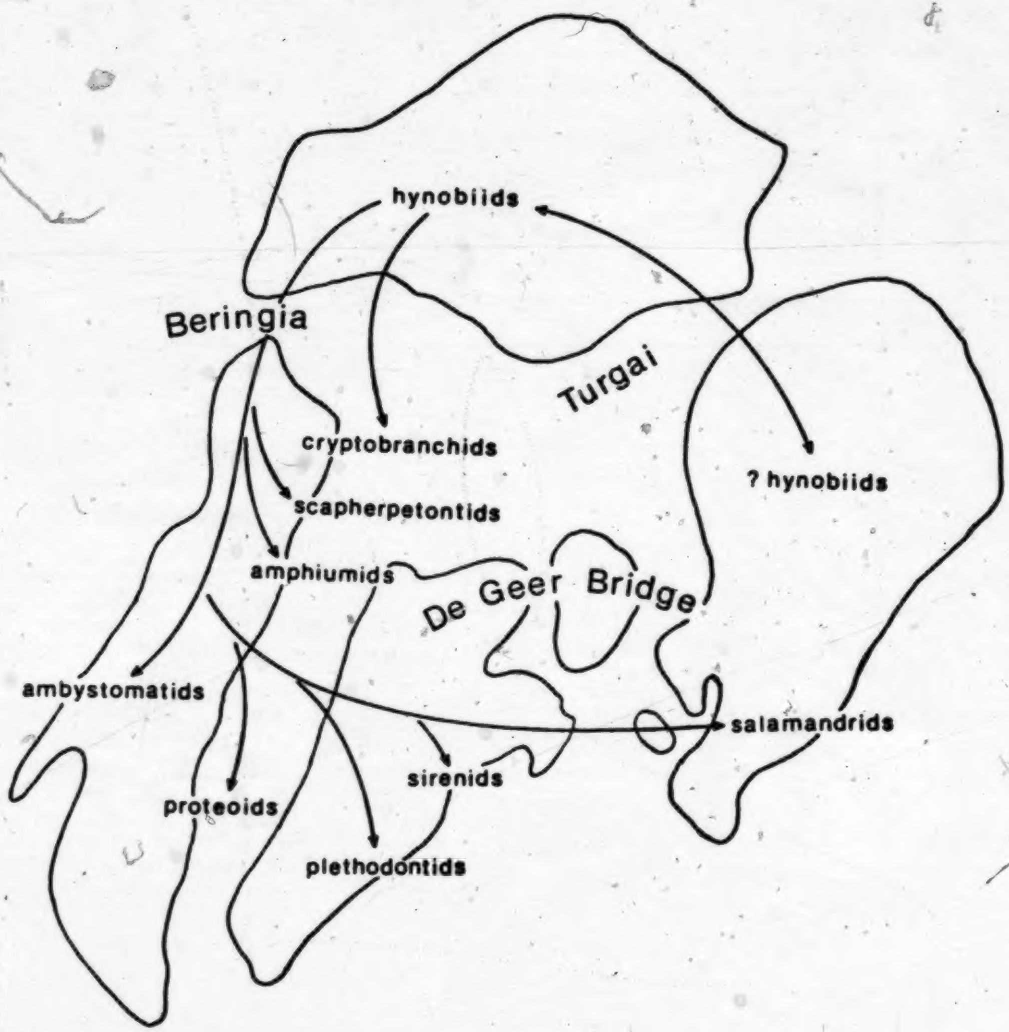

Sirenidae
Salamandridae
Plethodontidae
Proteidae
†Batrachosauroididae
Ambystomatidae
†Scapherpetontidae
Amphiumidae
Cryptobranchidae
Hynobiidae
NEOCAUDATA
ARCHAEOCAUDATA
?
?

Figure 105. Tentative dispersal patterns within the order Caudata, shown on a polar sketch of the northern hemisphere in Late Cretaceous time; see text for discussion.


hynobiids
Beringia
Turgai
cryptobranchids
? hynobiids
scapherpetontids
amphiumids
De Geer Bridge
ambystomatids
salamandrids
sirenids
proteoids
plethodontids